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Mechanisms underlying chasing behaviour of male blowflies

Doctoral Dissertation
by
Norbert Böddeker

Fakultät für Biologie
Universität Bielefeld

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Contents

Chapter 1

Zusammenfassung

Fliegenmännchen verfolgen im Kontext des Paarungsverhaltens andere Fliegen in sehr schnellen, visuell gesteuerten Flügen. Bei bis zu 10 Körperdrehungen pro Sekunde erreichen sie Winkelgeschwindigkeiten von bis zu 5000°/s. Das Verfolgungsverhalten von Fliegenmännchen stellt somit eine der virtuosesten visuell kontrollierten Verhaltensleistungen dar, die man in der Natur findet. Deshalb sind die zu Grunde liegenden Mechanismen und deren Zuverlässigkeit von großem Interesse. Im Rahmen meiner Doktorarbeit habe ich mit Hilfe einer quantitativen Verhaltensanalyse untersucht, welche visuellen Parameter des bewegten Zielobjekts für die Flugkoordination der verfolgenden Fliege wichtig sind. Darüber hinaus wurden die aus der Beschreibung des Verhaltens gewonnenen Hypothesen zur Flugsteuerung durch Modellsimulationen getestet.

In früheren Untersuchungen war es bislang nicht möglich gewesen, ein befriedigendes Modell für das Kontrollsystem des visuell kontrollierten Verfolgungsverhaltens der Fliege zu entwickeln. Dies lag in erster Linie daran, dass die untersuchten Verfolgungsmanöver, bei denen andere Fliegen verfolgt wurden, sich als so komplex erwiesen, dass es kaum möglich war konsistente Zusammenhänge zwischen visuellen Eingangsgrößen des Systems und den motorischen Ausgangsgrößen zu etablieren. Deshalb habe ich bei den meisten Verhaltensexperimente einen anderen Weg beschritten, um die visuellen Eingangsvariablen zu vereinfachen. Anstatt einer echten Fliege wurde dem Fliegenmännchen eine Attrappe als Zielobjekt angeboten, die sich in vom Experimentator vorbestimmter Weise bewegte. Es wurden schwarze, kugelförmige Attrappen unterschiedlicher Größe verwendet, die sich auf einer Kreisbahn mit unterschiedlicher Geschwindigkeit bewegten. Die Verfolgungsflüge wurden mit zwei Videokameras aus unterschiedlichen Richtungen gefilmt und die Flugbahnen von Fliege und Attrappe computergestützt rekonstruiert. Verschiedene retinale Variablen wie z.B. die Größe und Position der Attrappe auf dem Auge der verfolgenden Fliege konnten so berechnet und für die verschiedenen Versuchsbedingungen verglichen werden.

Charakteristik der Verfolgungsflüge

Fliegen verfolgen Attrappen von sehr unterschiedlicher Größe und Geschwindigkeit. Die Attrappen werden entweder gefangen oder bis zu 20 Runden verfolgt. Die Variation von Attrappengeschwindigkeit und -größe zeigt, dass vor allem Attrappen, deren Größe und Geschwindigkeit in etwa der von Fliegenweibchen entsprechen, nach kurzen Verfolgungsflügen gefangen werden, während größere oder schnellere Attrappen zwar verfolgt aber seltener gefangen werden. Größere Zielobjekte werden in einem größeren Abstand verfolgt als kleinere. In dieser Weise wird die retinale Größe von Zielobjekten, die nicht gefangen werden, weitgehend konstant gehalten, unabhängig von der absoluten Größe des Zielobjekts. Eine Attrappe einer bestimmten Größe wird bei einer größeren Geschwindigkeit in einem größeren Abstand verfolgt. Daraus resultiert, dass die retinale Größe des verfolgten Ziels mit zunehmender Geschwindigkeit abnimmt.

Modellanalyse

Auf der Basis der Verhaltensanalyse wurde ein phänomenologisches Modell entwickelt, das die wesentlichen Aspekte des Verfolgungsverhaltens von Fliegenmännchen in zwei Dimensionen erklären kann. Es wird angenommen, dass die Geschwindigkeit der Fliege von der retinalen Größe des Zielobjekts abhängig ist, während die Flugrichtung von der Position des Ziels auf der Netzhaut bestimmt wird. Neuronale Verarbeitungszeiten werden durch zeitliche Tiefpassfilter approximiert. Darüber hinaus werden kinematische Eigenschaften eines Inertialsystems mit Luftreibung simuliert.

Die Modellfliege zeigt ähnliche Eigenschaften wie die reale Fliege. Ob das Zielobjekt gefangen oder lediglich verfolgt wird, hängt in ähnlicher Weise wie in den Verhaltensexperimenten von dessen Größe und Geschwindigkeit ab, wie Modellsimulationen zeigen, in denen die Verfolgerfliege mit unterschiedlichen Ausgangspositionen und Ausgangsorientierungen startet. Es gibt also auch im Modell die beiden Verhaltensmodi, ohne dass eine explizite Entscheidungsinstanz implementiert worden wäre. In ähnlicher Weise wie bei der realen Fliege hängt die retinale Größe des Zielobjekts nicht von dessen absoluter Größe ab, während sie bei gegebener absoluter Größe mit zunehmender Geschwindigkeit der Attrappe zunimmt

„Sakkadisches“ Verfolgungsverhalten

Wenn Fliegenmännchen Ziele verfolgen, die nicht auf gleichförmigen Bahnen fliegen, sondern scharfe Kurven fliegen, findet man bei der Verfolgerfliege sogenannte Körpersakkaden – sehr schnelle Drehungen um die Hochachse, die auch im Spontanflugverhalten ohne ein verfolgtes Ziel auftreten. Auch die Virtuelle Fliege zeigt ähnliche Sakkaden. Da keine Mechanismen zur Generierung von Sakkaden in dem Modell implementiert wurden, kann geschlossen werden, dass diese Sakkaden die Konsequenz der Trägheit und der verschiedenen Zeitkonstanten der Fliege sind sowie der unregelmäßigen Flugbahn der vorausfliegenden Fliege sind.

Schlussfolgerungen und weitere Perspektiven

Die auf Grund von Verhaltensversuchen postulierten und im Modell implementierten visuellen Kontrollmechanismen sind hinreichend, um die Ergebnisse der Verhaltensversuche zu erklären. Die auf Grund von Verhaltensversuchen postulierten visuellen Mechanismen zur Steuerung des Verfolgungsverhaltens sind relativ einfach, wodurch die beispiellose Schnelligkeit und Virtuosität des Verfolgungsverhaltens gewährleistet wird. Fliegenmännchen fangen vor allem Ziele, deren Größe der von Artgenossen entspricht, während größere Ziele zwar verfolgt aber nicht gefangen werden. Diese Verhaltensentscheidung erfordert den Vergleich der intern repräsentierten Größe potentieller Paarungspartner mit der aktuellen sensorischen Information. Damit ist eine sehr konkrete Form von interner Repräsentation im Fliegengehirn zu fordern, die in zukünftigen Experimenten auf Einzelzellniveau untersucht werden soll.

Chapter 2

Introduction

Even relatively small animals are able to perform extraordinary things – at least if judged by comparison with man-made artificial systems. One example is the chasing behaviour of blowflies which outperforms with respect to its virtuosity any man-made autonomous system. Anyone who has ever observed blowflies chasing each other will be conversant with the breath-taking aerial acrobatics these tiny animals can produce. Whilst the human eye is scarcely capable of even following their flight paths, the chasing fly is quite capable of catching its speeding target. To do this it relies to a great extent on its large compound eyes, which give it almost all-round vision. The rapidly fluctuating pattern of brightness changes as sensed by the array of photoreceptors are delivered to the nervous system, processed in some ten milliseconds and then transformed into steering signals. How can the nervous system direct such a complex and highly precise behaviour? To answer this question it is important to discover from behavioural studies exactly how the "input variables", related to the image of the target on the pursuers retina, are translated into adequate behavioural responses. Having detailed knowledge on the way chasing flies use visual information it may be possible to determine what computational task the nervous system has to accomplish to make the sophisticated behaviour possible.

Not only blowflies, but many other insects follow moving objects and may eventually catch them. Predators like dragonflies, tiger beetles and mantids that prey on other insects, use visual mechanisms to track their moving targets (Olberg et al. 2000; Gilbert 1997; Rossel 1980). Visual tracking can also be part of the mating process in which the male captures the female. For instance, male flies of several genera chase females in acrobatic visually controlled flight manoeuvres. (Land & Collett 1974; Collett & Land 1975; Zeil 1983; Land 1993; Wagner 1986; Wehrhahn 1979; Wehrhahn et al. 1982). Male houseflies (*Musca domestica*) fixate the target in the frontal part of their visual field by generating sequences of saccadic turns with angular velocities of up to 5000°/s (Wagner 1986).

Although for chasing behaviour in flies it is generally assumed that the retinal

target position serves as an input variable of the pursuit control system, the way the retinal position error is transformed into torque is still controversial. On the one hand, smooth pursuit has been proposed (Land & Collett 1974; Collett 1980). On the other hand, a saccadic tracking strategy has been put forward (Wagner 1986). In the praying mantis both types of tracking strategies can be clearly distinguished. When sitting in ambush, the praying mantis fixates a target by rapid, saccade-like head and body movements. After being fixated, moving targets are held in the fovea either by smooth or by saccadic tracking eye movements. The degree to which either tracking strategy is employed depends on the features of the background, but also on the velocity of the target (Rossel 1980).

Pursuit of moving objects is not only a feature of insects. Rather primates and, in particular, humans are well known to fixate and to pursue moving objects by eye movements (Carpenter 1988). If an object moves only slowly, the eyes tend to fixate it by a saccade and then pursue it by smooth movements. If target motion is too rapid, smooth pursuit is interrupted by catch-up saccades.

All these studies reveal that, at least phenomenologically, similarly tracking strategies can be found in phylogenetically as distant animals, such as in insects and in humans. These common features are reflected in similar models that have been developed to describe pursuit systems in primates and in insects. In the fixation controller the retinal position of the target is determined and transformed into rotational velocity of the eyes, the head or, in case of insects, the entire body of the animal (Land 1992; Reichardt & Poggio 1976). Moreover, in primates, but also in insects, the retinal target velocity and even target acceleration may be a decisive visual cue in controlling smooth pursuit (e.g. Land 1992; Lisberger et al. 1987; Lisberger & Movshon 1999).

In two respects, pursuit of insects is likely to be more complicated than in primates. (i) If the target is to be caught by the pursuer as is frequently the case in insects, it is not sufficient for the animal to fixate it and to track it. The animal has also to control the forward velocity to reach its target. (ii) Several insect groups, such as flies or dragonflies, are able to follow targets, even when these move one order of magnitude faster than those targets humans are able to track.

It is the aim of this thesis to unravel those visual cues that are used by male blowflies to guide their acrobatic chasing manoeuvres. Because it has been problematic in previous studies to do this on the basis of the complex flight trajectories that are characteristic, if a blowfly pursues another fly, I employed a novel approach in most of my experiments. Instead of using real flies as targets, the complexity of the visual input was reduced by employing dummy targets moving on experimenter-controlled paths. The experimental analysis is com-

plemented by modelling. The modelling approach proved to be essential to test the viability of hypothesis concerning the mechanisms underlying chasing behaviour in a rigorous way.

The experiments were done on blowflies, because blowflies are well amenable to experimental analysis both at the behavioural and the neuronal level (reviews: Borst & Haag 2002; Egelhaaf et al. 2002; Egelhaaf & Borst 1993; Egelhaaf & Kern 2002; Hausen & Egelhaaf 1989). Moreover, in male flies sex-specific specialisations have been found at the level of the compound eye, and also in the nervous system (Burton et al. 2001; Gilbert & Strausfeld 1991; Gronenberg & Strausfeld 1991; Hardie 1986; Hausen & Strausfeld 1980; Hornstein et al. 2000; Land & Eckert 1985; Strausfeld 1991; Wachenfeld 1994). These sex-specific neurons are likely to represent a good starting point for future electrophysiological analyses.

My thesis will be subdivided into three parts.

- In the first part, the chasing system of male blowflies will be analysed by video techniques to find out which visual cues, available during chasing manoeuvres, play a role in mediating chasing behaviour.
- In the second part, a phenomenological model of the control system of chasing behaviour will be developed on the basis of the behavioural experiments. The model will be shown to be sufficient to explain all relevant behavioural features.
- In the third part, it will be shown that this model does not only account for chasing behaviour as characterised under the simplified stimulus conditions as used in my systems analysis, but also for complex features, such as saccadic tracking, as is characteristic of chases were a real fly serves as a target.

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Chapter 3

Chasing a dummy target: smooth pursuit and velocity control in male blowflies

Male blowflies chase and catch other flies in fast acrobatic flights. To unravel the underlying control system, we presented a black moving sphere instead of a real fly as pursuit target. By varying the size and speed of the target, this paradigm allowed a systematic analysis of the decisive visual determinants that guide chasing behaviour. Flies pursue targets of a wide range of sizes and velocities. The percentage of pursuits resulting in target capture decreases with increasing target size and speed. Chasing male flies adjust their forward velocity depending on the retinal size of the target, suggesting that retinal size is a relevant input variable of the control system. The chasing fly focuses the target with great accuracy in the frontal part of its visual field by means of a smooth pursuit control system using the retinal position of the target to determine the flight direction. We conclude that for a comprehensive understanding of chasing control, different time lags in the control systems of angular and forward velocity as well as the impact of inertia on fly movements need to be taken into account.

Introduction

To catch females and to mate with them, male flies engage in high-speed aerial chases involving virtuosic visually guided behaviour (Land & Collett 1974; Wehrhahn *et al.* 1982; Wagner 1986b). Given the great expenditure in terms of neuronal resources and energy consumption that is required to accomplish such an extraordinary form of mating behaviour, chasing appears to be a way to select the fittest males.

The functional significance of chasing behaviour is underlined by sexual dimorphisms in eye design and in brain structure, being most probably the neural substrate for chasing control (Hardie *et al.* 1981; Hornstein *et al.* 2000; . Hausen & Strausfeld 1980; Zeil 1983a; Strausfeld 1991). We analyse the chasing behaviour of

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blowflies (genus *Lucilia*), because it permits both filming of free-flying flies in relatively small flight arenas with sufficient spatial resolution and electrophysiological recordings of visual interneurons (Kimmerle & Egelhaaf 2000; Kern *et al.* 2001).

Apart from large hoverflies, which may reach their target via shortcuts by adopting an interception course (Collett & Land 1978), males of other fly genera fixate their target in the frontal visual field by body rotations thereby virtually copying the track of the leading fly (Land & Collett 1974; Wehrhahn *et al.* 1982; Wagner 1986b). It is generally agreed that the retinal position of the target serves as an input variable of the fixation control system. The way the retinal position error is transformed into torque is, however, not yet fully understood. On the one hand, continuous tracking analogous to human smooth pursuit eye movements has been proposed (Land & Collett 1974; Wehrhahn *et al.* 1982; Land 1993b). On the other hand, a saccadic tracking strategy reminiscent of human fixation saccades has been put forward (Wagner 1986b).

Without shortcuts chasing males will not reach their target unless they are faster. Still, it is not yet clear whether the fly controls its forward velocity relative to the target or chases the target in flat out pursuit (Collett & Land 1975; Wehrhahn 1979; Wehrhahn *et al.* 1982; Wagner 1986b).

The analysis of chases after real flies is complicated by the irregular flight manoeuvres of the target fly. Therefore, we simplified the conditions by using a dummy fly as target instead of a real fly. Flies have already been observed to chase moving targets, such as black painted peas (Collett & Land 1978; Zeil 1983b; Zeil 1986). By precisely controlling the movements of the target, we were able to, phenomenologically unravel the major constituents of the control system underlying chasing behaviour.

Methods

(a) Experimental procedure and set-up.

Experiments were done on at least 7 days old male blowflies of the genus *Lucilia* from laboratory stocks. For each set of experiments ten flies were kept in the flight arena for 2-7 days. The experiments were carried out with 5 different sets of male flies at temperatures between 25 and 35°C. Black painted glass spheres (diameter: 5, 8.3 and 13mm) served as dummy flies. They were glued to a thin transparent glass rod (length: 100mm) and moved on a circular track (radius: 100mm, speed: 1, 1.25, and 1.5m/s) in the x-y-plane (fig.1a). The dummy speeds were in the range of the speed of real flies. Combinations of dummy size

and speed were randomly chosen during filming sessions of 15-30 minutes.

The side walls of the cubic flight arena made of glass (length of the edges: 500mm) were covered with randomly textured tracing paper and illuminated from outside by four 500 W halogen lamps (luminance: 1200 cd/m^2 in the arena centre). The floor was transparent and the ceiling was homogeneously white. Chasing flights were filmed with two synchronised CCD-video cameras (image acquisition rate: 50 Hz; shutter time: 1ms) and stored in S-VHS format. One camera viewed the arena from below, the other from sideways through a hole in the wall texture. The optical axes of both cameras were aligned orthogonally to each other.

(b) Data analysis.

Sequences of interest were digitised with a DT 3155 (Data Translation Inc.) frame-grabber and stored in TIFF-format. 170 flights resulting in target capture were included into the analysis. Pursuits without capture (n = 184) were defined as chasing flights, if the male fly followed the target on its circular track for at least one lap. The position and orientation of moving objects in each image were detected by a specifically designed software, using standard image processing algorithms. The reconstruction of the 3D-trajectories (fig.1a) and all further data processing were done with Matlab 6.0 (The MathWorks, Inc.).

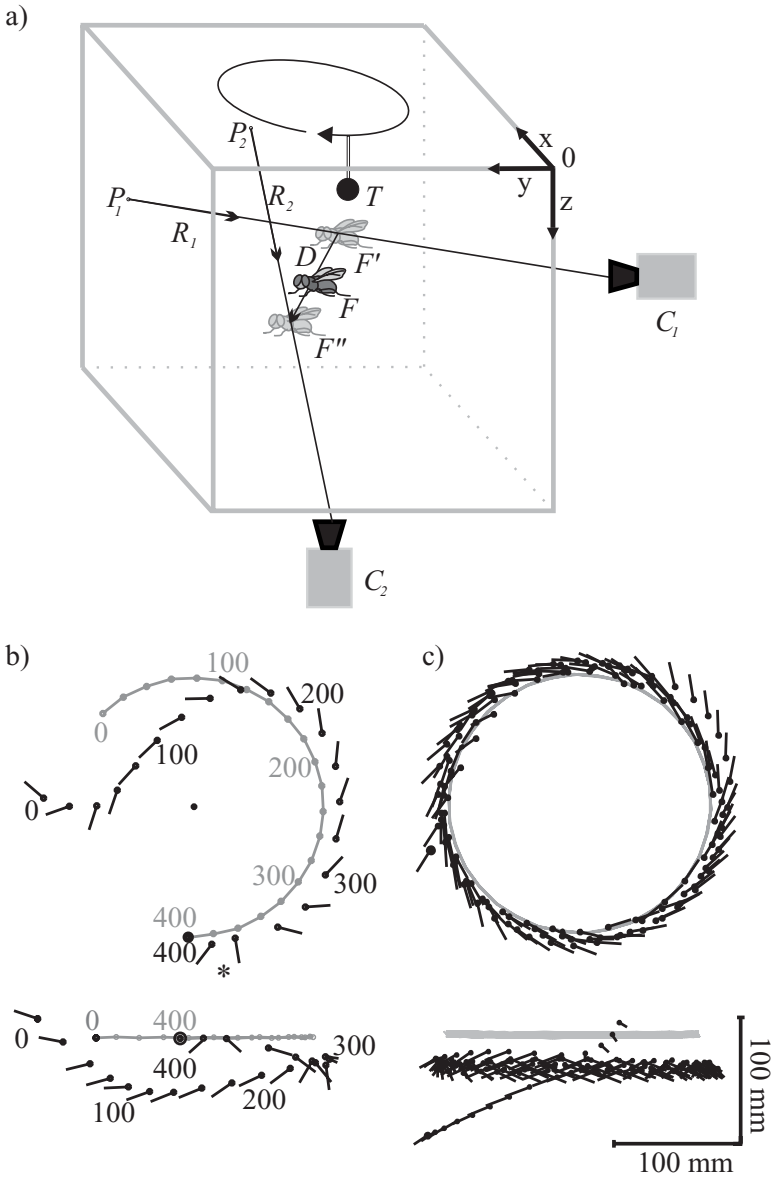
Although blowflies can move their head (Land 1973; Hengstenberg 1993), it is possible to estimate gaze shifts from body movements without recording the head movements. Yaw head rotations are usually in phase, though somewhat faster than yaw body rotations. Rotations of the head relative to the surrounding around the pitch and roll axes are generally small during flight (Schilstra & van Hateren 1998). The angle subtended by the fly's longitudinal body axis and a line connecting the fly and the target, therefore, represents an appropriate approximation of the azimuthal fixation error ("error angle") in a spherical fly-centred coordinate system.

(c) *Errors.*

The detectability of fly and dummy in video images is affected by:

(i) inhomogeneous illumination of the flight arena,
(ii) reflections on the wings and the fly's metallic green body surface
(iii) lens aberrations of the camera objectives,
(iv) noise in the CCD-chip of the camera.

Video tape jitter during digitisation adds to these error sources. To assess methodological errors, we reconstructed the given position and orientation of a perched fly. The yaw orientation of the fly was reconstructed with angular errors below 3° interquartile range (IQR) across time for stationary and for moving flies. When the same video sequence was repeatedly digitised, the time course of the reconstructed body orientation was different for each trial (IQR of 3°). Hence, the angular error is primarily due to tape jitter rather than to other sources. In contrast, the position error is not dominated by tape jitter, because it was possible to reconstruct the position with little errors (< 0.1mm) among repeated digitisations of the same frames. The position error increased with increasing eccentricity of the fly in the flight arena, but was always below 1.5mm. This position error is supposedly caused by distortions in the camera optics or by inhomogeneous illumination. Time dependent data (e.g. error angle, angular velocity) were not smoothed, because we do not have a priori knowledge about the frequency ranges of the relevant signals and the noise.


a)
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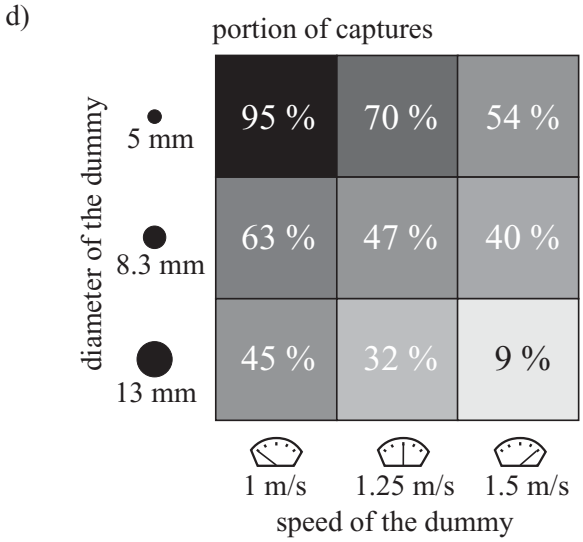
d)
portion of captures
95 %
70 %
54 %
63 %
47 %
40 %
45 %
32 %
9 %
diameter of the dummy
5 mm
8.3 mm
13 mm
1 m/s
1.25 m/s
1.5 m/s
speed of the dummy

Figure 1 (a) Experimental setup and reconstruction of three-dimensional trajectories. Two cameras (*C1* and *C2*) provide perspective views of the flight arena. The image coordinates are transformed into an orthographic three-dimensional coordinate system to avoid systematic positional errors in the excerpted flight trajectories. The procedure used for this coordinate transformation requires the determination of the view reference point (VRP) in each camera view, which coincidences with the camera position (*C1* and *C2*). The VRPs were calculated with the aid of a removable translucent cube (not shown) with 9 markers on the front and on the bottom side, the arena coordinates of which were known. The image coordinates of the fly in both camera views (F' and F'') were projected onto the back and top side of the arena (P_1 and P_2) in three-dimensional flight arena coordinates according to markers on the cube. Two vectors (R_1 and R_2) connecting P_1 and P_2 to the VRPs of the corresponding views were constructed in the arena coordinate system. The two vectors should intersect but due to small measurement errors they are skew. There is a point on each line that is closest to the other line. The midpoint of the segment connecting these points (D) gives the position of the fly (F) and can be calculated after solving the following three-dimensional set of simultaneous linear equations: $[P_1 + tR_1 + D = P_2 + uR_2]$ with two unknown variables t and u. The same procedure is used to determine the arena coordinates of the target (T). **(b)** Example of a reconstructed flight trajectory of a fly (black markers) capturing the target (grey markers) in top (upper panel) and side view (lower panel). The fly is indicated by the position of its centroid (circle) and the orientation of the body axis (line). The numbers denote corresponding positions of the fly and the target every 100ms. The asterisk denotes a sudden turn of the fly, before it catches the target. **(c)** Pursuit of the target without capture, plotting as in (b). **(d)** Dependence of target capture on target size and target speed. The percentage gives the portion of captures among all chases for a given combination of target parameters. The number of chases for each combination of target parameters ranges between 22 and 65. The total number of chasing flights is 354.

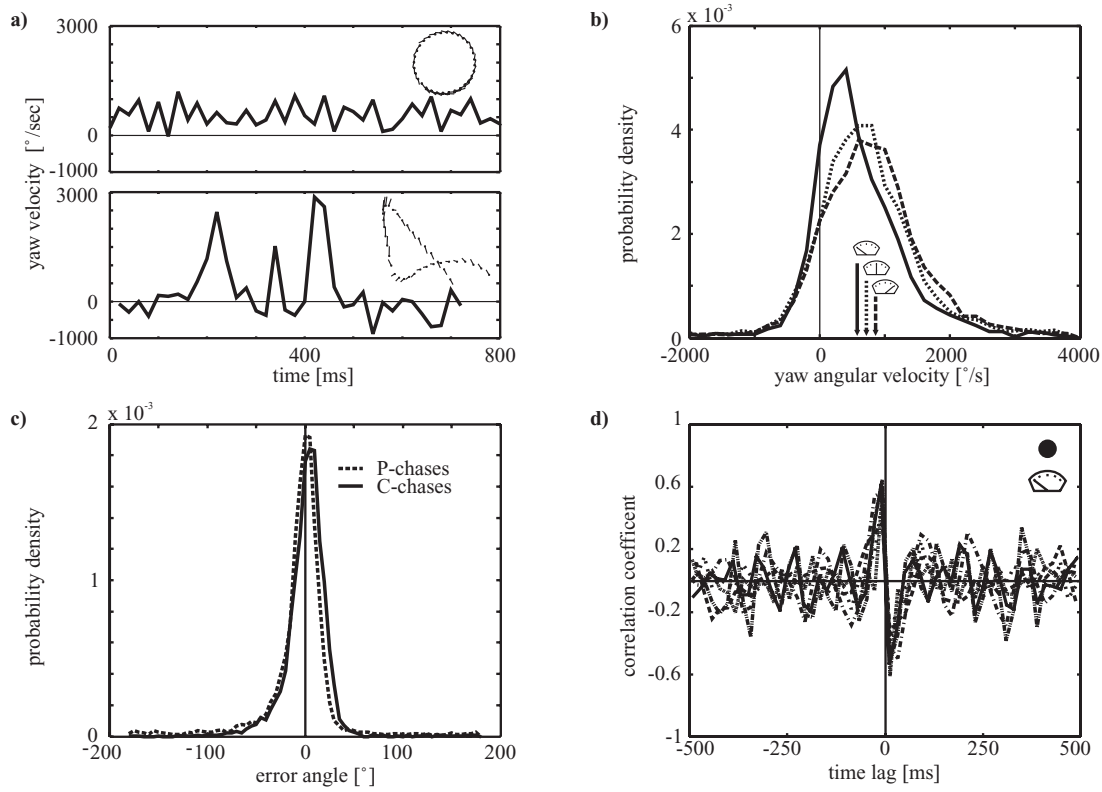

Figure 2 Control of yaw rotation. **(a)** Top: yaw velocity of a fly during an 800ms excerpt from the steady-state phase of the P chase example shown in fig. 1c. Bottom: yaw velocity of a fly during a cruising flight in the flight arena. Both yaw velocity traces are affected by noise as is described in the Methods section. Despite this methodical limitation the velocity peaks in the bottom trace due to body saccades are well detectable. Insets: body position and orientation of the longitudinal body axis of the fly every 20ms. (**b)** Probability density of the yaw velocity for all chasing flights grouped by target speed (indicated by arrows). A target moving at 1m/s on the circular track changes its yaw orientation with 573°/s (1.25 and 1.5m/s are equivalent to 716 and 859°/s, respectively). **(c)** Probability density of the error angle for 170 C chases (3169 data points) and 184 P chases (8234 data points). In each mode, data points of the error angle were pooled for all target speeds and sizes, because no obvious difference in the fixation performance could be detected with reference to different target conditions. (**d)** Cross-correlation of error angle and yaw velocity for six particularly long P chases (target size: 8.3mm, speed: 1m/s). The time lag that gives the highest correlation-coefficient is near the temporal sampling interval of 20ms in each of the six chases. The cross-correlogram that reveals the most pronounced periodicity is indicated by a solid line. The peak in the cross-correlograms shown is not the consequence of tape jitter (see Methods section), as tape jitter on its own leads to a much smaller correlation peak (not shown).

Results

Male flies chase targets of various sizes and speeds from below and behind. The target is either caught after short pursuits (median duration: 340ms, example in fig.1b) or is followed, sometimes for longer than seven seconds, without capture (fig.1c). Therefore, chasing flights might be classified into two categories: capture flights (C chases) and pursuit flights without capture (P chases). After the target has been captured, the male may stick to the target up to 50 laps. Whether or not the target is caught depends on its size and speed (fig.1d). Targets much larger than a real fly were chased some time, but were caught only seldom. Targets of the size of a conspecific (5mm) were captured more often than larger targets. This holds true for all tested target speeds. With increasing target speed, the frequency of capture decreases. Pursuit after targets moving at 2m/s occurred only seldom and never resulted in the capture of the target (data not shown).

While chasing the target, the fly continuously changes the orientation of its body long axis (fig.2a, top, fig.2b). Rapid saccade-like turns, which are characteristic of cruising flights and go along with large and brief yaw rotational velocity peaks (fig.2a, bottom; Wagner 1986a; Schilstra & van Hateren 1999), happened only occasionally during chases. Consequently, the distribution of yaw velocities has its peak around the angular velocity of the dummy target (fig. 2b). There is no pronounced peak at a speed of 0°/s, which would be expected if body rotations were saccadic with straight flight sequences between saccades. Hence, when chasing a target that changes its direction continually, chasing behaviour is reminiscent of a smooth pursuit system.

The chasing fly fixates the target in the frontal visual field during both P and C chases (fig.2c). There is no significant difference in the error angle between the two chasing modes. The median error angle is 1.5° in P chases (IQR of 20°) and 6° in C chases (IQR of 21°). Thus, in both modes the target is slightly shifted in the direction in which it would move on the eye if it were not fixated. To characterise the system controlling yaw rotations, the time lag between retinal error angle and the fly's yaw velocity was analysed by cross-correlation (fig.2d) for six particularly long sequences of smooth pursuit (length: between 1.5 and 7.5 s). The time lag cannot be resolved precisely, because it is of the same order of magnitude as the temporal resolution of the video technique (20ms). In any case, the time lag is short suggesting a quick transformation of the retinal error into body rotations. Periodicity in the cross-correlograms can be interpreted as oscillation of the underlying control system.

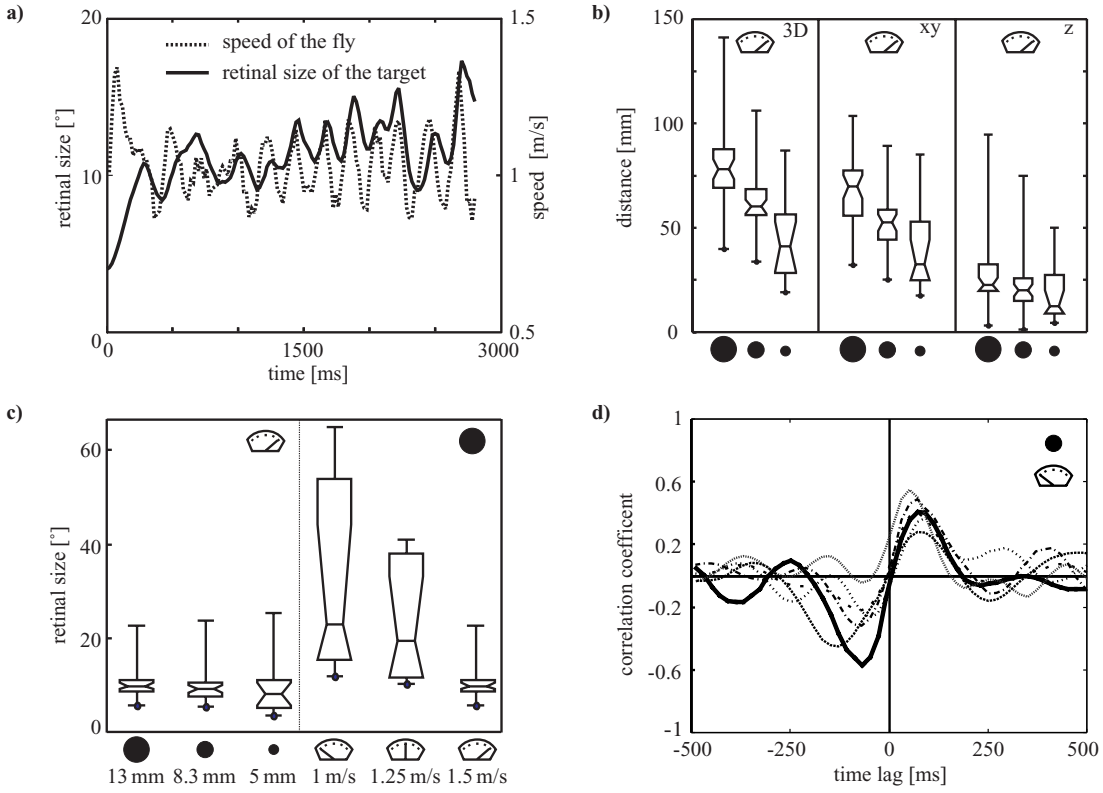

Figure 3 Control of forward speed. **(a)** Retinal size and speed of the fly during the P chase shown in fig. 1c. The speed of the chasing male is subject to fluctuations, that to some extent cause fluctuations in the distance between fly and target (not shown). Consequently the retinal size of the target also oscillates between local minima and maxima. **(b)** Box-and-whisker plots of the minimal distance between fly and target in each P chase after the 5, 8.3, and 13mm sized targets at a speed of 1.5m/s. The box has horizontal lines at the lower quartile, median, and upper quartile values. The lines extending from each end of the box show the extent of the rest of the data. The medians (central lines) of two box-and-whisker plots are significantly different ($p<0.05$) if the corresponding notches do not overlap (McGill *et al.* 1973). We did not calculate the mean distance to the target over the total flight episode, because this measure would have been much affected by the first approach of the target and the departure from the target, especially in short chases. We therefore calculated the median of all local minima of the time dependent distance in each chase. Left: three-dimensional distance, Middle: distance in the xy-plane. Right: difference of the z-coordinates of fly and target. For each target size between 48 and 65 P chases were included. **(c)** Box-and-whisker plots of the maximal retinal size (visual angle) of the target in each P chase. The retinal

size was calculated as the median of all local maxima of the time dependent retinal size for each chase. Left: differently sized targets at a speed of 1.5m/s (same chases as in b). Right: pursuits after the 13mm sized target at the three different speeds. **(d)** Cross-correlation between retinal size and fly speed for the same P chases as in fig. 2(d)**.** The cross-correlogram that reveals the most pronounced periodicity is indicated by a solid line.

The fly's speed correlates with the retinal size of the target, which is most noticeable during long P chases (fig.3a). To test whether the forward velocity relative to the target is controlled by the retinal target size, we measured the distance between fly and target for different target sizes and velocities. The larger the target, the larger is the distance between target and fly (fig.3b, left), which is mainly caused by variation of the horizontal distance (x-y-plane, see fig.1a) between fly and target (fig.3b, middle and right). As a consequence, the retinal target size is kept constant for a given speed (fig.3c, left). A control system with retinal size as input variable and the fly's speed as output can lead to this result. A time lag of 60-80ms between input and output of this hypothetical control system was determined for six long P chases by cross-correlating the time-dependent retinal target size and speed of the fly (fig.3d). Hence, forward velocity control operates with a larger time constant than turning velocity control. In P chases a target of given size is followed at larger distance, with increasing target velocity, and, thus, the retinal target size decreases (fig.3c, right).

The chasing male frequently flies slightly outside the circular track of the target (fig.1b and c). In C chases the fly eventually approaches the target from outside its track before capture. The fly's distance from the centre of the target's trajectory is larger for big targets than for small ones (fig.4a). During P chases the male may fly inside the circular target track for some time, but on average, the distance of the fly to the centre of the target track is moderately larger than the radius of the target track without significant dependency on target size or speed (median difference: 0.5-8mm, not shown).

The fly's speed is faster before catching large targets than before catching small targets (fig.4b). This finding is surprising, since, on first glance, there is no need to approach large targets faster than small ones. It should be noted that large targets are not always followed at higher speed than small targets, but only in those cases when the target is caught. As already stated above, capture of large targets happens only relatively rarely (fig.1d).

Before catching the target, the chasing fly changes its orientation in the horizontal plane and, concomitantly, deviates from the target's direction of movement by sometimes more than 90° (see asterisk in fig.1b). To quantify this behaviour, we calculated δ, which is the angle subtended by the fly's longitudinal body axis and the targets instantaneous flight direction in the horizontal plane. (see inset figure 4*c*). δ increases with increasing retinal target size and, thus, with decreasing distance between fly and target before the dummy is caught (fig.4c). Similar changes in δ are found during P chases while the fly approaches the target and the retinal target size thus increases (fig.4c).

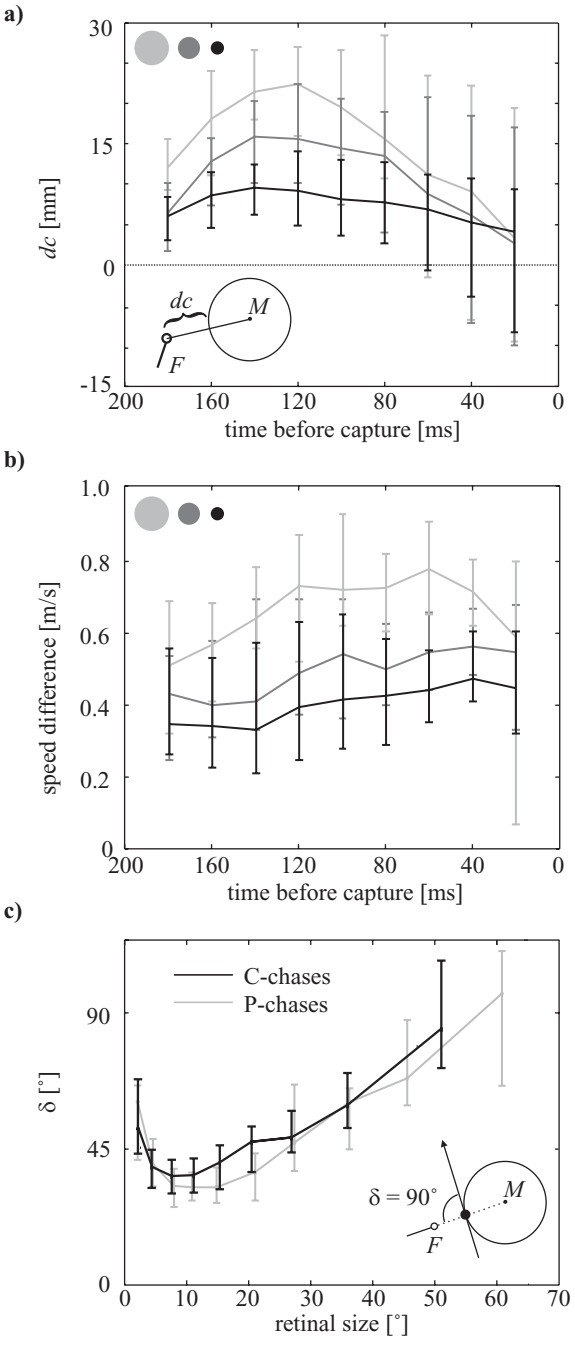

Figure 4 Features of the flight trajectories. **(a)** The variable *dc* quantifies whether the fly (*F*) is inside or outside of the circular target track. It is calculated by subtracting the radius of the target track from the distance between the fly and the midpoint (*M*) of the target track (see inset fig. 4a). Since we found no significant relation to target speed, the medians and quartiles of *dc* of all C chases (n = 170) were grouped with reference to the absolute target size and plotted vs. time for every sampling point during the last 180ms before capture. The absolute size of the target is indicated by the grey-level of the lines (see inset). **(b)** Speed difference between fly and target in C chases during the last 180ms before capture, for differently sized targets. Data pooling and plotting as in (a). **(c)** δ is the angle subtended by the fly's longitudinal body axis and the targets instantaneous flight direction in the horizontal plane. If the fly (*F*) flies tangentially to the target's track δ is 0°, if the fly's long axis points towards the centre of the track δ is 90° (see inset). δ is plotted vs. retinal size of the target averaged over all C (black) and P chases (grey).

Discussion

Male blowflies exhibit two behavioural modes when chasing a dummy fly. The target is either caught after relatively short pursuit flights (”C chases”) or the target is followed for up to several seconds on precisely controlled tracks without being caught (”P chases”). Since male flies do not only chase females, but also other males (Wagner 1986b) as well as black spheres, they are most likely unable to distinguish between the different types of targets without close contact. This is not surprising if one considers the coarse spatial resolution of the fly’s eye (Land & Eckert 1985).

Other fly species also exhibit two modes of chasing behaviour although these seem to play a different functional role as those of *Lucilia*. Male *Poecilobothrus* pursue at close distance females during courtship behaviour ("shadowing"), whereas other males are chased in pursuits resulting in head-on clashes (Land 1993a). Chasing of *Syritta* also includes shadowing that often culminates in a rapid dart towards the leading fly after it has settled (Collett & Land 1975).

The two chasing modes of *Lucilia* can parsimoniously be explained as the consequence of one single control system. This system is calibrated to control the capture of targets of proper size and velocity, but can be deluded if the target is either larger or faster than conspecifics. Under the artificial conditions of our experiments targets larger or faster than conspecifics often resulted in prolonged pursuits without capture. Since in natural situations potential targets usually do not move on regular tracks as the artificial target in our behavioural experiments, they may not be followed for a long time. The hypothesized pursuit system controls in parallel the rotational velocity and the forward velocity of the fly.

Control of yaw rotation

The control of yaw rotation in male *Lucilia* is organised in a similar way as proposed for the male-specific pursuit systems of other flies (Land & Collett 1974; Collett & Land 1975; Srinivasan & Bernard 1977; Wehrhahn *et al.* 1982; Poggio & Reichardt 1981; Wagner 1986b; Land 1993b). Moreover, yaw control even of female *Musca* in fixation tasks has been attributed to a similar mechanism (Virsik & Reichardt 1976). In all these systems, the target is detected at some retinal position and elicits a turning response towards the target. Within certain limits, the turning response increases with increasing deviation of the target from the frontal midline of the head (”error angle”). In order to maintain

fixation of a moving target, the error angle is converted into yaw rotation. Occasional deviations of the body axis direction from the flight direction (fig.1b) can be attributed to inertia (Boeddeker in prep.; Wagner 1986a).

Chasing flies are able to change their flight direction gradually when following a target moving on a smooth track. However, during cruising flight flies usually change course by short and rapid body saccades (Schilstra & van Hateren 1999). The gaze shifts of male flies, therefore, might be accomplished in a similar way as in primates and humans, i.e. in a smooth way when pursuing a target and by saccades when exploring a visual scene. Nonetheless, saccade-like turns of flies occur also during pursuit of real flies (Wagner 1986b) and occasionally during the smooth pursuit of dummy targets. We will show in a subsequent paper (Boeddeker in prep.) that these saccade-like turns are not necessarily generated by a saccadic tracking system, but can be explained as the consequence of a smooth pursuit system, provided that time constants and the inertia of the fly are taken into account.

Control of forward speed

Male *Lucilia* always approach the target from behind and from outside the circular track (fig.4a). Hence, *Lucilia* has to fly faster than its target to catch it. During P chases, male flies, on average, do not fly faster than their target, although their flight motor would enable them to do so. Instead, the forward velocity goes down when the retinal size exceeds a certain threshold and increases when the retinal size of the target is small. Hence, retinal size of the target appears to be a decisive input variable for forward velocity control in chasing behaviour. The smaller retinal size of fast targets compared to slow targets during P chases can also be traced back to the relation between the retinal size of the target and the speed of the fly. If a target of given absolute size moves at higher velocity, the fly needs to fly faster to follow it. As flight speed and retinal size are thought to be related inversely, this can only be achieved at a smaller retinal size.

At first sight, the conclusion that the chasing fly decelerates at a critical retinal target size, raises the question of how the chasing fly will ever be able to catch its target. As catching females is a prerequisite of mating, a velocity control system resulting in P chases where the target is only followed but not caught seems paradox. Can targets of the size and speed of conspecifics only be caught by inactivating the control of translational velocity during the final approach of the

target? To answer this question one has to consider that any neuronal control system requires time for information processing and, thus, the response is delayed relative to the stimulus. Moreover, inertia prevents the fly from adjusting its velocity immediately to the current retinal target size. Consequently, after the motor command for deceleration is given when the retinal size exceeds a critical value, the chasing fly retains its velocity for a while. This implies that a fly approaching a small target may be able to reach the target and catch it before the command to decelerate becomes effective. In contrast, when approaching a large target, deceleration is initiated at a large distance, though, at the same retinal target size as in the case of a small target. As a consequence, deceleration may become effective too early, and the target is followed without being caught because the fly is ”trapped” by its control systems.

Conclusions

The existence of C and P chases does not necessitate separate control systems. Several experimental findings allow us to underline this assumption.

(i) Small targets are caught most often, as the speed control system ”allows” a closer approach.

(ii) Large targets are only caught, if the fly is much faster than the target during the final approach. This might be essential, since only at a high velocity the pursuer is able to overcome the distance to the target, before the motor command to decelerate is becoming effective. Otherwise, the target will not be caught which then would result in a P chase.

(iii) The flight manoeuvre quantified by δ can be explained in both chasing modes as the consequence of interaction between target fixation , motor force reduction, and the remaining impetus of the fly. When during P chases the retinal size increases, δ (see fig.4c) increases in a similar way as during C chases. This takes place at a larger distance, which then results in missing the target.

We will show in a subsequent paper by model simulations that a control system with retinal size and position as input variables can account for most features of *Lucilia* chasing behaviour and will discuss this hypothesis in the context of the available literature (Boeddeker in prep.).

What may be the advantage of a translational control system that initiates deceleration of the chasing fly at a critical retinal target size, although it may prevent the male from catching targets? On the one hand, this peculiar feature prevents the fly from catching too large targets (such as hornets). On the other hand, capture of an appropriate target might be improved if the male does not crash into it with full speed but rather slows down before contact. This deceleration may facilitate a graceful embrace of the potential Ms Right.

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Chapter 4

Steering a virtual blowfly: Simulations on visual pursuit

The behavioural repertoire of male flies includes visually guided chasing after moving targets. The visuomotor control system for these pursuits belongs to the fastest found in the animal kingdom. We simulated a virtual fly, to test whether or not experimentally established hypotheses on the underlying control system are sufficient to explain chasing behaviour. Two operating instructions for steering the chasing virtual fly were derived from behavioural experiments: (i) The retinal size of the target controls the fly's forward speed and, thus, indirectly its distance to the target. (ii) A smooth pursuit system uses the retinal position of the target to regulate the fly's flight direction. Low-pass filters implement neuronal processing time. Treating the virtual fly as a point mass, its kinematics is modelled in consideration of the effects of translatory inertia and air friction. Despite its simplicity, the model shows behaviour similar to that of real flies. Depending on its starting position and orientation as well as on target size and speed, the virtual fly either catches the target or follows it indefinitely without capture. These two behavioural modes of the virtual fly emerge from the control system for flight steering without implementation of an explicit decision maker.

Introduction

Male flies chase moving targets in fast acrobatic flights. If the target is caught and turns out to be a conspecific female, the flies possibly mate (Land & Collett 1974; Wehrhahn et al. 1982; Wagner 1986). The goal of our investigations is to comprehensively understand the functioning of the system controlling the virtuosic pursuit behaviour. In a first step towards this goal we analysed chasing behaviour experimentally (Boeddeker et al. 2003). In the present account we compare the behavioural performance of real flies with the performance of a

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virtual fly which incorporates our experimentally established hypotheses for the control system underlying chasing.

The blowfly *Lucilia* is our experimental animal, because it is well amenable to behavioural and neurophysiological techniques. We performed a behavioural systems analysis using a black sphere instead of real flies as target, which was moved on a circular track in a small flight arena (Boeddeker et al. 2003). By this approach it has been possible to systematically control and manipulate the visual input of the pursuing fly; even under free-flight conditions.

The main findings were as follows:

(i) The chasing fly keeps the retinal position of the target in the frontal field of view by smooth rotation about the vertical head axis.

(ii) Depending on the size and the speed of the target, the fly exhibits one of two chasing modes: the target is either caught after relatively short pursuit flights or followed by the chasing fly for up to several seconds on precisely controlled tracks without being caught.

(iii) During such ”unsuccessful” chases, the fly follows a large target at a greater distance than a small target. In this way the retinal size of the target is kept approximately constant during pursuit irrespective of its absolute size. However, the retinal size at which the target is followed decreases with increasing target speed.

Pursuit behaviour in flies has already been modelled at different levels of explanation, ranging from phenomenological models (Land & Collett 1974; Reichardt & Poggio 1976) to neuronal network models (Missler & Kamangar 1995). The latter model was inspired by the anatomy of the fly’s visual system and general properties of fly visual interneurones. All these models focus on the visual control of flight direction which enables the chasing fly to fixate the target in the frontal field of view but omit the control of forward velocity. The artificial hoverfly developed by Cliff (1992) comprises not only a neural network controller performing foveal fixation of a target, but additionally contains a network that regulates the distance to the target. This artificial hoverfly was based on hypotheses on visual flight control mechanisms in *Syritta pipiens* (Collett & Land 1975). A similar approach was taken in a recent study (Anderson & McOwan 2003) implementing a computational model of a stealth strategy inspired by the apparent mating tactics of male hoverflies (Srinivasan & Davey 1995).

None of these pursuit models is designed to explain the chasing behaviour of *Lucilia* and, in particular, its two chasing modes. This is accomplished by the

virtual blowfly introduced here. Another feature of our virtual blowfly, not taken into account in previous pursuit models, is the simulation of the effects of translatory inertia and air friction on locomotion.

We use a minimal set of operating instructions to generate fly-like chasing behaviour. One might think of two separate control systems underlying chasing behaviour in *Lucilia*: one mediating pursuit before capture and one for the guidance of target capture. However, our behavioural analysis suggests that both behavioural components can be explained parsimoniously as the consequence of a single control system for speed control. We suppose that the control system is tweaked to steer a flight course resulting in the capture of targets of proper size and speed, i.e. the size and speed of female *Luciliae*. The real and the virtual fly can be deluded if the target is either larger or faster than conspecifics.

Design of the virtual fly

In our behavioural experiments, chasing flies mainly moved in a plane below and parallel to the plane in which the target moved (Boeddeker et al. 2003). This feature was particularly obvious for extra long chases without target capture, during which chasing flies rarely varied their flying altitude. Rotations of the head relative to the surroundings around the pitch and roll axes are generally small during flight (Schilstra & van Hateren 1998). Therefore, we restricted the mobility of our virtual fly to rotation about its vertical axis and to translation in the horizontal plane, with gaze direction being equivalent to body orientation. These three degrees of freedom are sufficient to enable the virtual fly to generate those steering behaviours we found in real flies chasing a dummy target on a circular track.

We implemented two visual pathways in our virtual fly: one for target fixation (figure 1a, right) and one for speed control (figure 1a, left). Whereas the retinal size of the target controls the forward speed of the virtual fly, the position of the retinal image of the target determines the fly's flight direction. First-order low-pass temporal filters are applied to the outputs of both visual pathways, mimicking neuronal processing and muscle reaction time. In accordance with our experimental results, the time constant in the target fixation pathway was 15 ms, and thus much shorter than the time constant of the pathway for speed control (80 ms). The outputs from each pathway form the 'intended' vector of locomotion of the virtual fly, as it is represented at its motor output. However, as a consequence of friction and inertia, this intended vector of locomotion does

not exclusively determine the actual trajectory of the virtual fly. A third module emulates the kinematics of fly body movements and determines the virtual fly's actual position and orientation in the next simulation step. Data is updated 1000 times per simulated second.

Speed control.

Viewed from the pursuer's position, the image of the target subtends a visual angle ρ ('retinal size'). The retinal size depends on the absolute size of the target and on the distance between pursuer and target. Our behavioural analysis revealed a systematic relation between absolute target size and the distance the fly keeps to the target during non-capture chases (Boeddeker et al. 2003). As a consequence, the retinal size is almost constant for a given target speed, independent of the absolute target size. Therefore, the output of the virtual fly's speed controller (*s*) was assumed to depend on retinal target size (ρ). Male *Luciliae* follow a fast moving target at a larger distance and thus see it at a smaller retinal size than a slowly moving target (Boeddeker et al. 2003). Therefore, we assumed the output of the speed controller to decrease with increasing retinal target size. Since targets at a large distance are too small to be perceptible for a fly, the controller output should then not be affected by target size but adjust a "spontaneous" speed 'S_g'. The relationship between the retinal size of the target and the output of the speed controller is given by the following equation with model parameters S_g , S_v and ρ^* . These parameters jointly determine the gain and the location of the maximum of the speed controller's characteristic curve.

$$s(t_{n+1}) = \begin{cases} S_g & if\ \rho \le 0.5° \\ \rho(t_n)\, S_V\, e^{-\rho(t_n)/\rho^*} + S_g & if\ \rho > 0.5° \end{cases} \quad (1)$$

Target fixation.

The angle subtended by the fly's longitudinal body axis and the line connecting the fly with the target represents the deviation of the target position from the frontal midline of the pursuer's head ('error angle'). The error angle is defined in a fly-centred polar coordinate system with 0° pointing directly ahead. A fixation controller, converting in each simulation step the error angle (φ) into angular speed of the pursuing virtual fly in the horizontal plane (Δα), can be formalised by equation (2):

$$\Delta\alpha(t_{n+1}) = \begin{cases} 0 & if\ \rho \le 0.5° \\ G \sin(\varphi(t_n)) & if\ \rho > 0.5° \end{cases} \qquad (2)$$

G determines the gain of the orientation change. It is zero, if the retinal size of the target is smaller than 0.5°. To compute the orientation of the virtual fly in the next simulation step ($\alpha(t_{n+1})$) the low-pass filtered output of the fixation controller ($\Delta\alpha(t_{n+1})$) is added to $\alpha(t_n)$, i.e. the orientation in the previous time step. Given the small size of a fly its angular momentum can be neglected (Reichardt & Poggio 1976; Land & Collett 1974)

Virtual fly kinematics.

To steer the fly, the output signals of the fixation and speed controllers are used to compute one vector for each simulation step: the intended velocity ($\vec{i}$). The direction of this vector is determined by the fixation controller, its length by the speed controller. A velocity change in real flies is induced by forces that act on the fly's body. In the physical world the fly's locomotion is affected by momentum and viscous air damping. Especially the latter is difficult to determine exactly. We therefore follow an approach that has been used to steer autonomous agents in computer animations (Reynolds 1999). Treating the virtual fly as a point mass, its kinematics is modelled by the computationally cheap forward Euler integration. For each simulation step the new velocity vector $\vec{v}$ is given by the following formula:

$$\vec{v}(t_{n+1}) = (1-M)\,\vec{v}(t_n) + M\,\vec{i}(t_{n+1}) \qquad \text{with } 0<M<1 \quad (3)$$

To what extent the intended velocity determines the virtual fly's trajectory and the trajectory is predetermined by the preceding flight path, can be adjusted by the parameter *M*. *M* is used to fit the trajectories of the virtual fly to those of real flies. Adding the "new" velocity vector to the "old" fly position results in the position of the virtual fly in the next simulation step; the direction of $\vec{i}$ corresponds to the gaze direction (figure 1a, bottom).

In accordance with our behavioural experiments, the simulated targets (sizes: 5mm, 8.3mm and 13mm) were moved on a circular track (radius: 100mm, speeds: 1 m/s, 1.25 m/s, and 1.5m/s), always starting from the same position. The virtual fly was released from 441 evenly distributed starting positions in a simulated 300x300 mm² sized flight arena. At each start position the virtual fly started with the spontaneous velocity (0.8 m/s) at four different angles (0°, 90°, 180°, 270°) of gaze direction. When the virtual fly came closer to the target than the target radius plus 5 mm, which corresponds approximately to the length of the fly's legs, we assumed that the target was caught and the simulation was terminated.

Results

Adjustment of model parameters

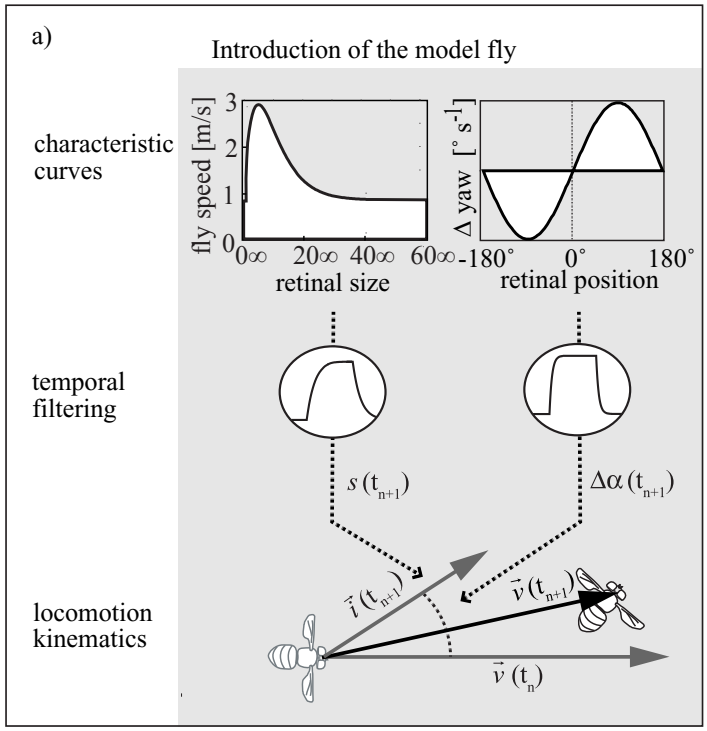
The behaviour of the virtual fly can be manipulated by variation of seven parameters: the two first-order low-pass filter time constants acting on fixation (τ_f) and speed control (τ_v), the gain of yaw rotation (G), the movement coefficient (M), and three parameters characterising the transfer function of the speed controller (S_g, S_v, ρ^*). We adjusted these parameters within the constraints set by our behavioural analysis (Boeddeker et al. 2003): (1) The intended speed cannot exceed 3 ms^{-1} or fall below 0.8 ms^{-1} (2) The time constants in the fixation (τ_f) and speed controller (τ_v) were set to 15ms and 80 ms, respectively. The gain for yaw rotation (G = 0.125) was adapted to produce stable fixation behaviour and to prevent the rotational speed from exceeding 5000°s^{-1}. To obtain realistic trajectories *M* was set to 0.0455. *M* values near 1 would mimic an unrealistic fly that is not affected by viscous air damping or inertia (figure 1d). The time constant of the low-pass filter in the speed branch (τ_v) must be nonzero to enable the virtual fly to catch the target. Setting τ_v to zero and M to 1 will always result in endless pursuit without target capture (figure 1e). Capture behaviour (figure 1b) is strongly related to the parameters of speed control which we parameterised

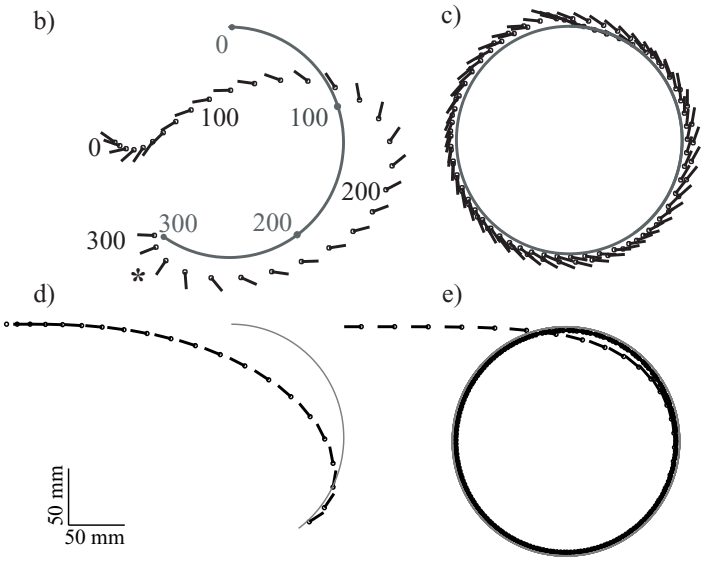
with S_g = 0.8 ms-1, S_v = 67, and ρ^* = 0.0865. It should be noted that the qualitative features of the virtual fly's behaviour are very robust to variations of most of these parameters. We chose a set of parameters that leads to results qualitatively similar to those obtained in behavioural experiments on real flies, as regards the percentage of target captures and the shape of trajectories. Parameterised in this manner, the virtual fly was tested to determine whether or not it also reproduced other aspects of chasing behaviour we characterised in behavioural experiments

Performance of the virtual fly in explaining behavioural results

For a given target size and speed, small variations in the virtual fly's starting position and orientation can determine whether or not the target is caught. When we tested the virtual fly from different starting positions with different body axis angles the target was either caught after short pursuits (example in figure 1b) or followed indefinitely without capture (figure 1c) until the simulation was stopped. In analogy to the behavioural experiments, simulated chasing flights can therefore be classified into two categories: capture flights (C chases) and pursuit flights without capture (P chases). The probability of target capture depends on target size and speed (figure 1f) in qualitatively the same way as found in real flies (Boeddeker et al. 2003). Targets much larger than a real fly were chased, but were only seldom caught. Fly-sized targets (5mm) were caught more often than larger targets. This holds true for all tested target speeds, although with increasing target speed, the frequency of capture decreases.

While chasing the target on its circular track, the fly continuously changes the orientation of its body long axis to keep the target centred in the frontal part of the visual field (figure 2a). Despite the fact that we built a continuous controller, occasionally rapid saccade-like turns occur, identifiable by a brief rotational velocity peak. These go along with rapid body orientation changes. Saccade-like turns occur, at the beginning of a chase (figure 2a, arrow), when the virtual blowfly approaches the target very closely but misses it (P chases, not shown), or shortly before capture in C chases (figure 1b, asterisk). In P chases the virtual blowfly will reach a steady state after some time with respect to its angular velocity and retinal error angle (figure 2a).





f)

portion of captures

diameter of the dummy	1 m/s	1.25 m/s	1.5 m/s
5 mm	100 %	100 %	100%
8.3 mm	97 %	85 %	74 %
13 mm	84 %	21 %	10 %

speed of the dummy

Figure 1 (a) Layout of the virtual fly. The output of the virtual fly's speed controller (pathway on the left) depends on retinal target size and determines the absolute value of the fly's speed vector for the next simulation step ($s(t_{n+1})$). The fixation controller (pathway on the right), converts in each simulation step the error angle into angular speed of the pursuing virtual fly ($\Delta\alpha(t_{n+1})$). First-order low-pass temporal filters are applied to the outputs of both visual pathways mimicking neuronal processing and muscular reaction time. The filtered outputs from each pathway form the 'intended' vector ($\vec{i}\,(t_{n+1})$) of locomotion of the virtual fly. A third module emulates the kinematics of fly body movements and determines the virtual fly's velocity in the next simulation step ($\vec{v}\,(t_{n+1})$) as the weighted sum of the actual fly velocity $\vec{v}(t_n)$ and the 'intended' velocity vector. **(b)** Example of a simulated C chase. Trajectory of a fly (black markers) capturing the target (grey markers). The virtual fly is indicated by the position of its centroid (circle) and the orientation of the body axis (line) every 10 ms. The numbers denote corresponding positions of the fly and the target every 100ms. The asterisk denotes a sudden turn of the fly, before it catches the target. **(c)** Example of a simulated pursuit of the target without capture (P chase). **(d)** An unrealistic flight trajectory with a virtual fly that is not affected by viscous air damping or inertia (M in eq. 3 is set to 1). **(e)** The same virtual fly as shown in (d) but additionally τ_v is set to zero which will always result in endless pursuit without target capture. **(f)** Dependence of target capture on target size and target speed. The virtual fly was started from 441 different positions and from each position with 4 different body axis orientations. The target was either caught after short pursuits (see figure 1b) or followed indefinitely without capture (see figure 1c) until the simulation was stopped. The percentage gives the portion of captures among all chases for a given combination of target parameters.

The error angle is constant during the steady state of P chases and the mean rotational velocity of the virtual blowfly exactly equals the rotational velocity of the target after several seconds (figure 2c, vertical lines on the x-axis; values: 573°s^{-1}, 716°s^{-1}, 859°s^{-1}). The value of the steady state retinal error is slightly shifted in the direction in which the target would move on the eye if it were not fixated. The error slightly increases with increasing target speed (figure 2b, vertical lines on the x-axis; values: 4.5°, 5.75°, 6.9°). In C chases qualitatively the same dependence on target velocity is found in C chases for the error angle and the yaw velocity. However, in contrast to the steady-state of P chases, the distributions of the error angle (figure 2b) and the yaw velocity (figure 2c) are broad. This is mainly a consequence of geometry: unless the fly is not directly heading toward the target, the error angle will, on average, increase the more for a given translational movement the closer the virtual fly is to the target. Since the error angle is the signal that drives rotational velocity, larger turns are likely to occur if the virtual fly is close to the target (e.g. figure 1b, asterisk). The time lag between retinal error angle and the fly's rotational velocity, as determined by cross-correlation, is -12ms (figure 2d). Periodicity in the cross-correlograms results from oscillation of the underlying fixation controller.

After the onset of P chases, the retinal size at which the target is seen by the virtual fly and, accordingly, the translational velocity which is controlled by it, tend to oscillate until they settle to a steady state level (figure 3a). In the steady state, the retinal target size is independent of the absolute target size (figure 3c) implying that larger targets are followed at a larger distance than smaller ones. However, retinal target size decreases with increasing target velocity (figure 3c). These features of the virtual blowfly's behaviour agree well with the performance of its biological counterpart (Boeddeker et al. 2003). Since in C chases the target is eventually caught, the retinal size inevitably increases during an approach. The speed of the virtual fly initially increases above target speed, but it slows down when the retinal target size gets too large just before catching the target (figure 3b). The time lag of about -75ms between the retinal target size and the blowfly's speed, as determined by cross-correlation, can be attributed to the locomotion kinematics of the virtual fly and the simulated neuronal processing time lag of the speed controller (figure 3d). This time lag is, in accordance with our experimental results (Boeddeker et al. 2003), shorter than the time lag for fixation control.

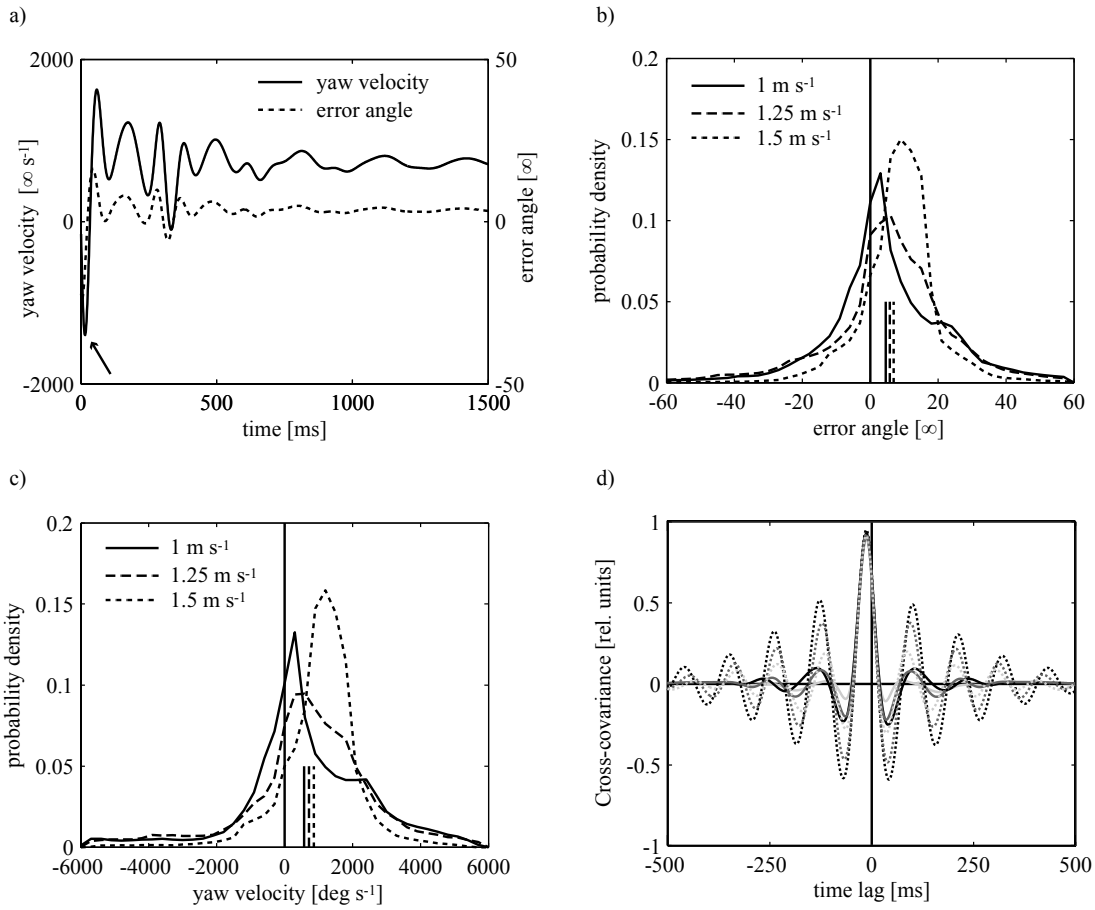


Figure 2 Control of yaw rotation. **(a)** Rotational velocity of a fly (solid line) and error angle of the target (dotted line) during the first 1500 ms of the P chase example shown in figure 1c. (**b)** Probability density of the error angle for C chases. The steady state error angles during P chases after targets of different speeds are indicated by lines on the x-axis by the same linestyles for different target speeds as for C chases. **(c)** Probability density of the yaw velocity for all C chases grouped by target speed (indicated by linestyle). A target moving at $1ms^{-1}$ on the circular track changes its yaw orientation with $573°s^{-1}$ ($1.25ms^{-1}$ and $1.5ms^{-1}$ are equivalent to $716°s^{-1}$ and $859°s^{-1}$, respectively). In the steady state of P chases the mean rotational velocity of the virtual blowfly exactly equals that of the target (lines). (**d)** Mean cross correlation of error angle and yaw velocity during the first 1500 ms of P chases after the 13 mm (solid lines) and 8.3 mm (dotted lines) sized targets. The black lines indicate a target speed of 1 m/s, (dark-grey: 1.25; pale-grey: 1.5 m/s).

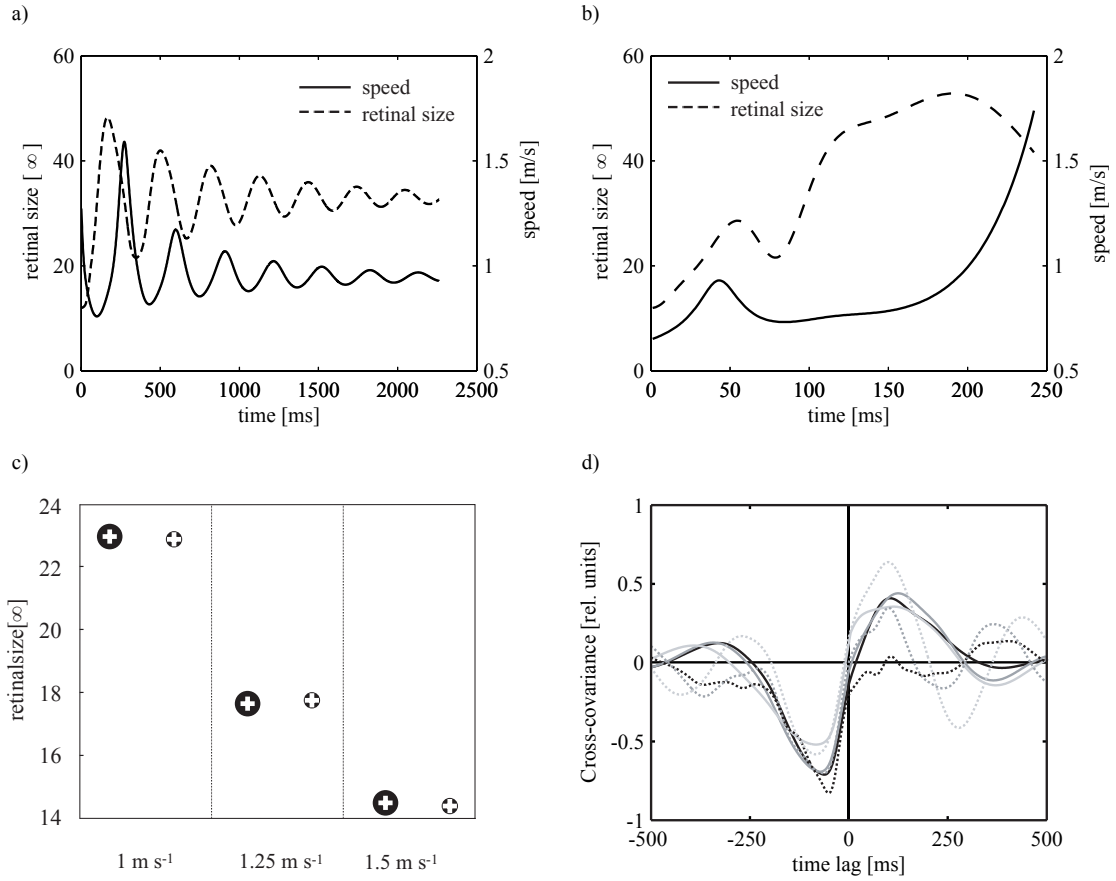


Figure 3 Control of forward speed. **(a)** Retinal size (solid line) and speed of the fly (dotted line) during the P chase shown in figure 1c. The same variables from the C chase shown in figure 1b are plotted in **(b)**. **(c)** The retinal size (visual angle) at which the target is seen by the virtual fly settles to a steady state level during P chases (see figure 3a). The steady state retinal size in P chases is independent of the absolute target size (small symbols: 8.3 mm; large symbols: 13 mm) for a given speed. Targets of 5 mm size were always captured (see figure 1f). **(d)** Cross-correlation between retinal size and fly speed for P chases, plotted as in figure 2(d).

Discussion

We propose a chasing controller for a virtual blowfly that is able to chase moving targets with an efficiency similar to that of real flies. Following the principle of parsimony, we built this virtual blowfly as simple as possible. The virtual blowfly is equipped with two visual control systems for steering motor actions, one that controls flight speed, depending on retinal target size, and another that mediates turns depending on the location of the target in the visual field. It turned out to be relevant for the proper performance of the virtual blowfly to take into account time lags due to neuronal processing as well as the locomotion kinematics of blowflies. Most important, the virtual blowfly shows a bifurcation into two behavioural modes similar to real blowflies: The target is either caught (C chases) or pursued without capture (P chases). Such a dual response mode comes about without assuming an explicit decision maker. Chasing behaviour of blowflies as one of the most virtuosic visually guided behaviours found in the animal kingdom might therefore be regarded as an example of complex behaviour that emerges from simple rules.

Differences between the behaviour of virtual and real blowflies – limitations of the model

Real flies show much variability at all levels of information processing (reviews: Juusola et al. 1996;Warzecha & Egelhaaf 2001). Nonetheless, the proposed virtual blowfly was implemented without internal noise sources. Thus, its behaviour is entirely deterministic. The variability in chasing performance even for a given size and speed of the target (figure 1f) results only from the variation of starting positions and orientations of the fly relative to the target. If noise sources were inserted into the virtual blowfly, the simulated catching probabilities may well match the experimentally measured probabilities even in quantitative detail. Additionally, a realistic simulation of motion blur, that occurs in the blowfly's retina as a consequence of the temporal properties of its photoreceptors, would impair visual acuity for moving targets of small retinal size (Korenberg et al. 1998, Juusola & French 1997). The capture probabilities especially of small targets might then be lower than without taking motion blur into account.

Since so far the virtual blowfly is completely deterministic and entirely driven

by its sensory input, it will pursue every target of appropriate size in its range of sight. Hence, the model can be expected to match the chasing behaviour of a real blowfly that is "motivated" to chase. For instance chasing in flies younger than five days occurs very seldom even if a target of appropriate size is present (own observation). Moreover, the "motivation" to pursue a target may change during a pursuit manoeuvre, for instance if it is unsuccessful for some time. In contrast, during P chases the virtual blowfly will follow the target forever, because changes in “motivation” were not modelled.

Very little is still known about the actuator dynamics of flying blowflies. Additionally the unsteady aerodynamics of insect flight complicate a realistic simulation of the virtual blowfly’s trajectories (Ellington 1999; Dickinson et al. 1999). Since our intention was to test *visual mechanisms* underlying flight control, we refrained from simulating flight dynamics and used a comparatively computationally cheap kinematic locomotion model.

Relationship to other models of pursuit behaviour

Control of rotation

A principal task of pursuit systems is to minimise the angular error between the actual and the desired retinal position of a target. Formalisms describing pursuit of moving targets in various animals use as input to the fixation controller the position, the velocity and partly also the acceleration of the target’s retinal image (Land & Collett 1974; Reichardt & Poggio 1976; Virsik & Reichardt 1976; Collett & Land 1975; Lisberger et al. 1987; Land 1992, Rossel 1980, Krauzlis & Stone 2003). In previous studies on chasing behaviour of various fly species, it has been proposed that the fixation controller relies on both retinal position of the target and on the direction of its motion. Whereas the position system is assumed to induce turns toward targets in the lateral visual field (Srinivasan & Bernard 1977), targets in the frontal field of view are assumed to be processed by a motion-sensitive system (Land & Collett 1974; Wehrhahn et al. 1982; Wagner 1986). However, model simulations suggest that only one visual cue, i.e. either retinal position of the target (Cliff 1992) or retinal motion (Missler & Kamangar 1995), is sufficient to explain many aspects of chasing behaviour of the simulated fly species.

Although blowflies tend to change their flight direction during spontaneous flights by brief and rapid body saccades (Schilstra & van Hateren 1998; Schilstra & van Hateren 1999), flies are able to change their flight direction also gradually

when following a moving target (Boeddeker et al. 2003). In this respect, the viewing strategies of blowflies are reminiscent of those of primates (Carpenter 1988). For convenience, we used a sinusoidal transfer function to transform retinal position into rotational velocity. Other functions are likely to lead to similar results, as long as two conditions are met: (i) The induced rotational velocity needs to increase with increasing error angle up to a certain retinal position. (ii) To avoid a discontinuity in the posterior field of view which would reduce the stability of fixation control, the induced rotational velocity needs to decrease for targets at more lateral retinal positions. As will be shown in a subsequent paper (Boeddeker & Egelhaaf 2003), saccadic tracking, as can be observed in real flies pursuing conspecifics (Wagner 1986), can be explained as an emergent property of this type of fixation control even when implementing only a smooth pursuit system into the virtual blowfly. Although the fixation controller relies exclusively on retinal target position, so far, the performance of the virtual blowfly might be improved by additionally taking into account the target's retinal velocity (Land 1992). This can be expected, at least, if the target moves like real blowflies on more complicated tracks than the circular ones used in our behavioural systems analysis (Boeddeker et al. 2003).

Control of forward speed

The speed controller of the virtual blowfly does not estimate its distance to the target explicitly, but uses the retinal size of the target as relevant input variable. In this regard our virtual blowfly is similar to the artificial hoverfly proposed by Cliff (1992). These simple mechanisms, thus, confound targets of different absolute size. Hence, targets of different absolute size will lead at different distances to a given speed of the virtual blowfly, similarly to real blowflies (Boeddeker et al. 2003). However, if a target of given size moves at a higher velocity, it is followed by both the virtual and the real blowfly at a larger distance than a slowly moving target. This characteristic feature is an inevitable consequence of the shape of the speed controller's characteristic curve, and particularly its descending slope at large retinal target sizes (figure 1a).

Significance of time constants in the control system

The performance of chasing blowflies can be explained if neuronal processing time and the time a steering command requires to become effective are taken into account. As a consequence of these time constants, the chasing blowfly retains its velocity for a while after the motor command for deceleration or accel-

eration is given. A blowfly approaching a small target may thus be able to reach the target and to catch it before deceleration gets too large. In contrast, when approaching a large target, deceleration is initiated at a large distance, though, at the same retinal target size as in the case of a small target. As a consequence, deceleration may become effective too early and the target is followed without being caught. The blowfly is ”trapped” by its control system. This feature can explain why large targets are caught less frequently than small ones.

The potential neuronal substrate of chasing behaviour

Male-specific neurons in the fly’s brain are the most likely substrate mediating chasing behaviour (Hausen & Strausfeld 1980; Zeil 1983; Gilbert & Strausfeld 1991). On the whole, the characteristics of the chasing control system that were derived on the basis of behavioural experiments and tested in the present study are in accordance with what is known about the properties of these neurons. Most male-specific neurons receive input from the dorso-frontal area of the retina which is used to keep the image of a conspecific centred during pursuit. Photoreceptors in this part of the retina have a higher spatiotemporal resolution than those in other parts of the eye (Land & Eckert 1985; Burton et al. 2001). The responses of some male-specific neurons depend on retinal target size (Gilbert & Strausfeld 1991; Gronenberg & Strausfeld 1991; Wachenfeld & Hausen 1994) in a similar way as does the forward speed of our virtual blowfly. Hence, these neurones may play a role in speed control. Computations similar to those proposed for the speed controller of the virtual blowfly are performed by the so-called lobula giant movement detector of locusts (Gabbiani et al. 1999; Rind & Simmons 1999), though in a different behavioural context (Robertson & Johnson 1993; Gray et al. 2001).

It is still not entirely clear whether male-specific neurons of flies are direction-selective or mainly represent the retinal position of a moving target (Gilbert & Strausfeld 1991; Wachenfeld & Hausen 1994). Although the turning responses of our virtual blowfly were assumed to depend only on retinal target position and not on target velocity, this issue is not entirely clear at the behavioural level (see above). In the next step of our analysis we are heading towards modelling the neuronal computations underlying fixation and speed control. These simulations will be based on experiments where male-specific neurons will be characterised with stimuli as seen by the blowfly in behavioural situations (see Lindemann et al. 2003 for an explanation of the approach).

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Chapter 5

Chasing behaviour of blowflies: A smooth pursuit tracking system generates saccades

Chasing behaviour of flies is one of the most acrobatic behaviours that can be observed. Male flies pursue other flies in complicated flight manoeuvres that are characterised by sequences of saccadic turns. It is analysed to what extent an autonomous virtual fly, originally designed to explain pursuit of smoothly moving artificial targets, can also account for saccadic tracking as observed during pursuit of real fly targets. A minimal set of operating instructions is incorporated in the virtual fly to generate fly-like chasing behaviour in model simulations. It is shown that the virtual fly does not only pursue smoothly moving artificial targets but also real flies flying on more complicated courses in a similar manner as do real flies. Although no saccade generating mechanism is implemented in the virtual fly, it can track realistically moving targets showing saccadic body movements. This performance relies (1) on the characteristic relation between retinal target position and the induced turning velocity and (2) on the implementation of inertia and time constants for turning velocity and forward velocity control. Thus, the dichotomy in the phenomenology of chasing behaviour—smooth pursuit and saccadic tracking—does not necessarily require two distinct control systems.

Introduction

When cruising around in an exploratory manner flies typically change their flight direction and, concomitantly, the direction of their gaze through a series of short and fast saccadic turns. In the intervals between these body saccades they fly relatively straight ensuring that gaze direction stays more or less constant (Wagner 1986b; Schilstra & van Hateren 1998). These sequences of straight flight are assumed to be under control of the visual system (Götz 1975; Land 1973; van Hateren & Schilstra 1999) and mechanosensory systems (Sandeman 1980; San-

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deman & Markl 1980; Gilbert & Bauer 1998; Chan et al. 1998). Saccades were concluded to be controlled visually and elicited by asymmetries in the optic flow pattern across both eyes (Tammero & Dickinson 2002).

The pattern of gaze control is similar in humans viewing a static scene or when fixing, for instance, a cup of tea (Land 1999). Gaze shifts in primates, including humans, result from rapid saccadic eye movements that direct the gaze to a new location. The gaze is held almost still during the intervening fixations by reflexes that stabilise the eye even when the head moves (for a review, see Carpenter 1988).

In primates a functionally different class of eye movements catch the image of a moving target and hold it steady relative to the eye, even if the observer and therefore the visual world moves. During these smooth pursuit eye movements a moving object is followed continuously. However, if target motion is too rapid or target contrast is too low smooth pursuit is interrupted by catch-up saccades which tend to fixate the target in the frontal visual field. Primates were long believed to be the only animals having the ability to perform smooth pursuit. Only recently smooth pursuit has been revealed also in cats (de Brouwer et al. 2001). Moreover, smooth pursuit is even found in insects, that are required by their visual ecology to track moving targets, for instance, to prey on smaller insects (dragonflies: Olberg et al. 2000), or to catch potential mates during courtship behaviour (hoverflies: Collett & Land 1975; houseflies: Wagner 1986; reviews: Land 1992; Land 1995). Interestingly, blowflies are able to follow targets that move one order of magnitude faster than those targets humans are able to track. For instance, male blowflies follow a target moving on a circular track in smooth pursuit (figure 1(a); Boeddeker et al. 2003). Smooth pursuit is characterised by continuous body rotation (figure 1(d)) matching the fly's yaw velocity to that of the target (figure 1(f)), to keep the target in the frontal visual field (figure 1c).

Pursuit of blowflies after smoothly moving targets, can be explained on the basis of a phenomenological model, the virtual fly (Boeddeker & Egelhaaf 2003): The retinal size of the target controls the virtual fly's forward speed and, thus, indirectly its distance to the target, whereas flight direction is controlled by the retinal position of the target. To account for the experimental data obtained with a smoothly moving target, neuronal processing time and the kinematic effects of translatory inertia and air friction had to be implemented in the virtual fly. In its current version, the virtual fly can only be expected to match the chasing behaviour of a real blowfly that is "motivated" to chase. Moreover, it does not care about any aspects of the visual surroundings despite visual information related to retinal target size and position. Nonetheless, the virtual blowfly can mimic all

relevant features of the flight trajectories of real blowflies chasing after a smoothly moving artificial target.

However, the trajectories of conspecific flies that are chased in the context of mating behaviour (example in figure1(b)), are much more erratic than the smooth target movements used in our previous systems analysis (Boeddeker and Egelhaaf 2003). Accordingly, pursuit of real flies is characterised by rapid saccade-like turns, that go along with brief rotational velocity peak (see figure 1f&h). These body saccades are apparently necessary to catch up with the target, if the retinal position of the target is not centred (figure1(d)). The control system underlying chasing behaviour in the housefly *Musca* was therefore suggested to steer the fly's flight direction by a saccadic control system (Wagner 1986a). Such a saccadic control system was assumed to translate a retinal input to adequate motor output not continuously, as would be done by a smooth pursuit controller, but only at discrete instants of time. Moreover, the input is assumed to be sampled only from time to time and the output to consist of pre-organised responses, i.e. the saccades without visually driven feedback (Wagner 1986a). In contrast to these conclusions on the housefly *Musca*, the behavioural analysis of chasing behaviour in the housefly *Fannia canicularis* (Land & Collett 1974), the dolichopodid fly *Poecilobothrus nobilitatus* (Land 1993), the hoverfly *Syritta pipiens* (Collett & Land 1975) and in blowflies of the genus *Lucilia* (Boeddeker et al. 2003) suggested that the tracking system is basically continuous in nature. Nonetheless body saccades occur occasionally during pursuit in most of the above mentioned flies.

Because saccadic and smooth pursuit strategies differ so much in their performance, they may be assumed to be mediated by fundamentally different control systems (review: Land 1992). The present paper starts off from a different perspective. Rather than assuming *a priori* different mechanisms underlying smooth and saccadic tracking in blowflies, we test to what extent the smooth pursuit system, we proposed for chasing of male blowflies after smoothly moving target (Boeddeker & Egelhaaf 2003) is able to account also for pursuit of realistically moving targets that may contain also sudden changes of flight direction as they result from saccades of the leading fly (figure 1b). The design and the parameters of the virtual fly we use here, are the same as in our previous study (Boeddeker and Egelhaaf 2003). The performance of the virtual fly, however, will be compared with an elaborated version of it. Fixation of moving targets will then be accomplished not only by a controller that uses the retinal position error of the target as input signal, but also target velocity. We wanted to test if an additional velocity input to the chasing control system can improve its

performance. This elaboration of the virtual fly has been motivated by two reasons: (1) The use of retinal target velocity, in addition to position error information, was found in previous model simulations to stabilise the performance of smooth pursuit systems (Land 1992). (2) The smooth pursuit system of primates uses target velocity as an important input variable (Rashbass 1961) and all current models of pursuit eye movements include a velocity servo Churchland & Lisberger 2001; Krauzlis & Lisberger 1994; Robinson et al. 1986)).

Whereas in primates smooth pursuit and saccadic tracking are assumed to be mediated by separate sensory and motor control systems, we present evidence that, at least in blowflies, both types of following responses can be produced by a single control system. We show by model simulations that saccadic changes of body orientation of the virtual blowfly emerge without an explicit saccade generator, if the target is displaced rapidly on the pursuing fly's retina. Thus, saccadic tracking in blowflies can be explained as an emerging property of a smooth pursuit system.

Results

We restricted the mobility of our virtual blowfly to yaw rotation and to translation in the horizontal plane, with gaze direction being equivalent to body orientation. These three degrees of freedom are sufficient to enable the virtual fly to generate those steering behaviours we found in real flies chasing a dummy target on a circular track (Boeddeker & Egelhaaf 2003). We refrained, so far, from simulating chases after targets, where the target fly alters its flight altitude very much.

We implemented two visual pathways in the virtual fly: one for target fixation (figure 2, upper pathway) and one for speed control (figure 2, lower pathway). The retinal size of the target controls the forward speed of the virtual fly. The position and angular velocity of the retinal image of the target determine the fly's intended flight direction. In order to mimic neuronal processing and muscle reaction time first-order low-pass temporal filters are applied to the outputs of both visual pathways. In accordance with our experimental results, the time constant in the target fixation pathway was 15 ms, and thus much shorter than the time constant of the pathway for speed control (80 ms). The outputs of each pathway form the 'intended' vector of locomotion of the virtual fly, as it is represented at its motor output. However, as a consequence of friction and iner-

tia, this intended vector of locomotion does not exclusively determine the actual trajectory of the virtual fly. A third module emulates the kinematics of fly body movements and determines the virtual fly's actual position and orientation in the next simulation step (illustrated in the box on the right half of figure 2). For details see Methods.

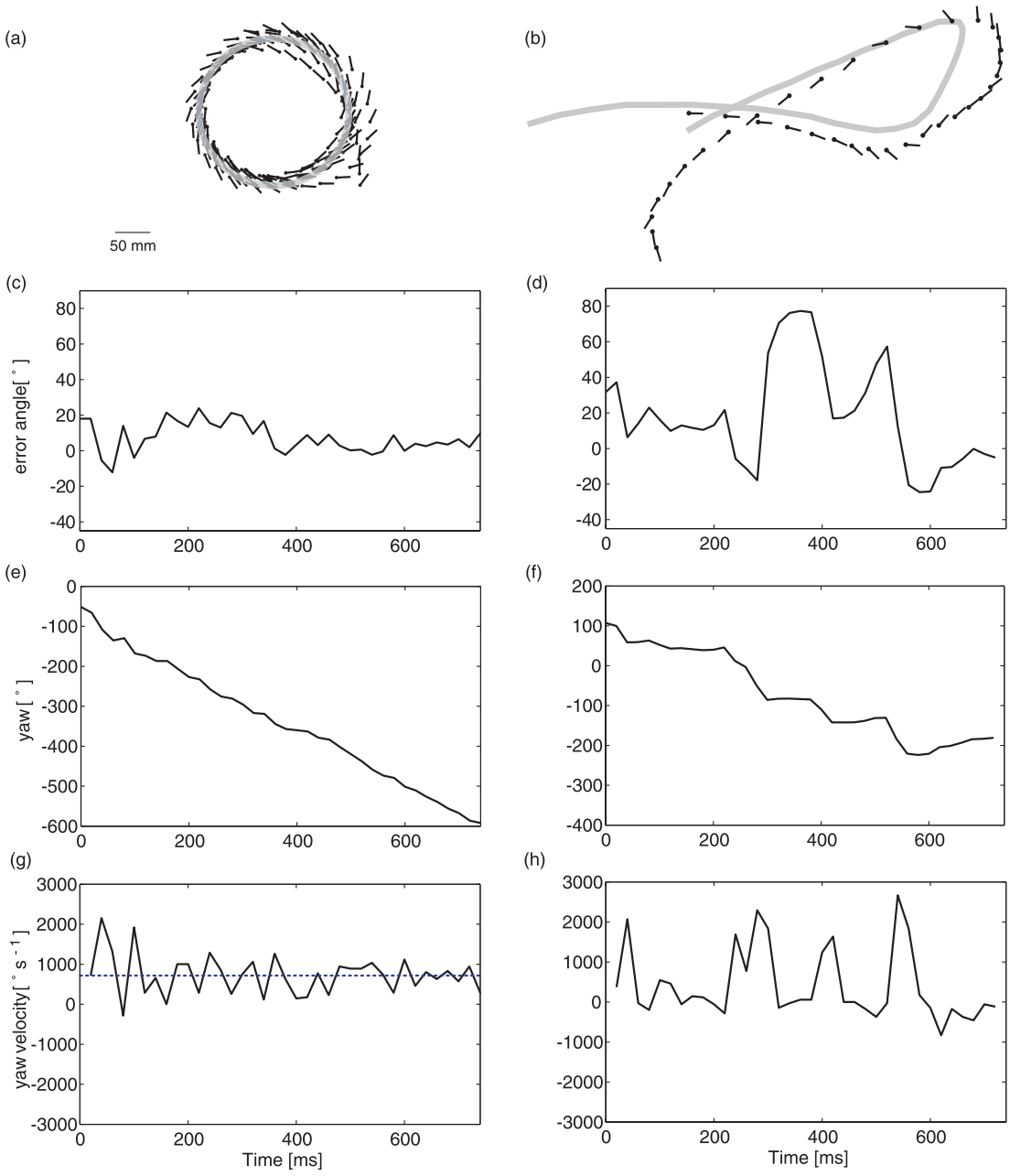

Figure 1 Saccadic and smooth tracking during chasing flights of male blowflies. Chasing flights were filmed with two video cameras (image acquisition rate: 50 Hz), allowing a computer aided three-dimensional reconstruction of the flight trajectories and the yaw orientation of the fly in an external coordinate system. For further details see Boeddeker et al. (2003). (a) Example in top view of a flight trajectory of a fly (black markers) chasing a black sphere (diameter: 8.3 mm) that moves at a speed of 1.25 m/s on a circular track in a horizontal plane (transparent grey line). The fly is indicated by the position of its centroid (circle) and the orientation of its body axis (line). The fly follows the target for 4 seconds. Every frame is shown. (b) Example of a flight trajectory of a fly chasing another fly in top view, plotted as in (a). To allow an easier comparison i.e. to have the same direction of target motion, the trajectories in (b) where vertically flipped before further analysis. Plots of the error angle (c & d), yaw orientation (e & f), and angular velocity (g & h) vs. time for the chase shown above each plot. In order to have the same time scale in all plots, only the first 740 ms of the chase displayed in (a) are shown in each plot of the left column. The rotational velocity of the dummy target ($716° s^{-1}$) is indicated by the dotted line in (f). All traces are affected by noise, primarily due to tape jitter rather (Boeddeker et al. 2003). Despite this methodical limitation the yaw velocity peaks due to body saccades are well detectable in (g).

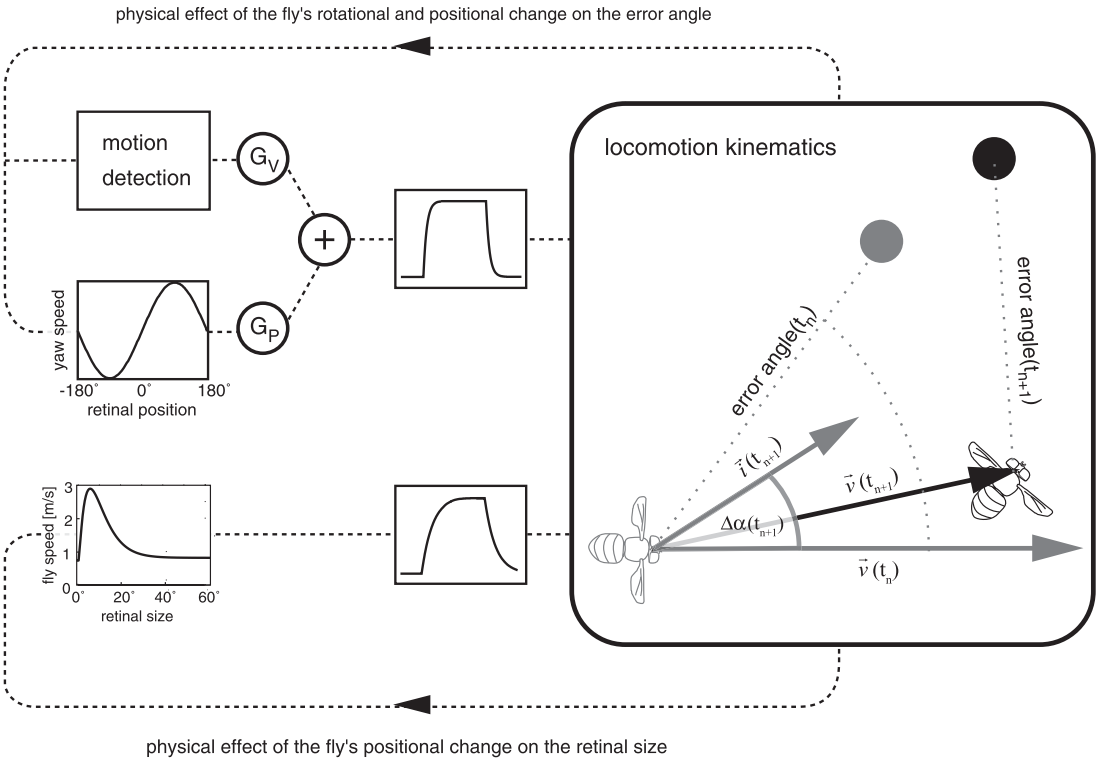

Figure 2 Sketch of the signal processing performed by the virtual fly. We implemented two visual pathways in our virtual fly: one for target fixation (upper pathway) and one for speed control (lower pathway). A further module that receives input from both pathways emulates the kinematics of fly body movements and determines the virtual fly's actual position and orientation in the next simulation step (box on the right half of the figure). The fixation controller, converts in each simulation step the error angle according to the characteristic curve shown in the box, weighted by G_P, and the retinal velocity, weighted by G_V, into angular velocity of the pursuing virtual fly: ($\Delta\alpha(t_{n+1})$). The output of the virtual fly's speed controller depends on retinal target size according to the characteristic curve shown in the box and determines the absolute value of the fly's speed vector for the next simulation step ($s\ (t_{n+1})$). First-order low-pass temporal filters are applied to the outputs of both visual pathways mimicking neuronal processing and muscular reaction time. The filtered outputs from each pathway form the 'intended' vector $\vec{i}(t_{n+1})$ of locomotion of the virtual fly. A third module emulates the kinematics of fly body movements and determines the virtual fly's velocity in the next simulation step ($\vec{v}\ (t_{n+1})$ as the weighted sum of the actual fly velocity $\vec{v}(t_n)$ and the 'intended' velocity vector.

Pursuit of a realistically moving target

A virtual fly, that uses for locomotion control only information on the retinal size and the position error of the target ('position-only servo') cannot only pursue smoothly moving targets (Boeddeker & Egelhaaf 2003), but also a target that moves like a real fly (figure 3a). The trajectory of the virtual fly is very similar to the trajectory of a real fly chasing the leading fly on an almost triangular flight path (cp. figure 1 b). While chasing the target, the fly adjusts the orientation of its body long axis to keep the target centred in the frontal part of the visual field (figure 3b). Despite the fact that we implemented a continuous controller, rapid saccade-like turns occur, that are characterised by brief rotational velocity peaks (figure 3c,d, arrows). This characteristic stays qualitatively the same when the position-only servo is augmented by a velocity input, as long as the gain of the velocity input of the resulting position-plus-velocity servo is relatively small (G_v = 0.0015). Although the fixation controller is stabilised as a consequence of a small velocity gain (see below), it apparently has no major impact on the overall performance of the virtual fly (figure 3e-h). Increasing the gain of the velocity signal to higher values, will impair the performance of the virtual fly compared to a real fly (G_v = 0.005; figure 3i). Fixation of the target in the centre of the visual field is poor and saccade-like turns are absent (figure 3j-l). We conclude that fixation control relies strongly on the position error and might be improved by taking into account the image velocity of the target, as long as the velocity input is not too strong. Since we did not implement an explicit saccade generator in the virtual fly the question needs to be answered, what causes the saccadic body orientation changes of the virtual fly.

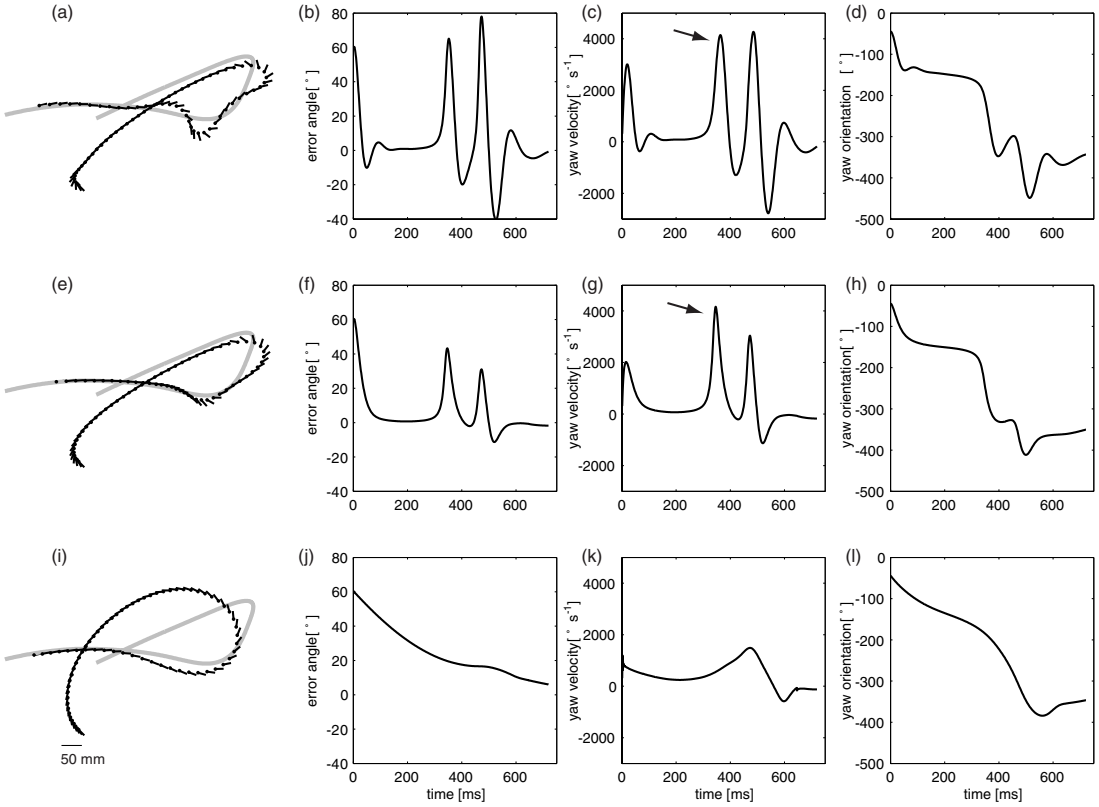

Figure 3 Chasing of a realistically moving target by the virtual blowfly. The gain factor for retinal velocity input relative to the fixation controller is varied. The data shown in (a-d) are from a virtual blowfly with the "position-only servo", i.e. the virtual blowfly steers its flight direction only by minimising the error angle. (a) Trajectory of the virtual fly chasing the target (plotted as in 1a). After sharp turns of the target, the virtual fly makes saccades, but tends to overshoot the target and then makes a correctional movement. This behaviour leads to a curved path and fluctuations of the error angle (b) and yaw velocity (c). The yaw orientation (d) of the fly changes in a stepwise manner in a similar way as in real flies chasing a conspecific (figure 1a). If the virtual blowfly uses a "position-plus-velocity servo", i.e. it uses both position and velocity information, (G_V: 0.015), flight performance is stabilised by reducing the overshooting of the target (e-h). Increasing the gain of the velocity signal to higher values (G_V: 0.005) leads to rather smooth flight trajectories and an elimination of saccades. This chasing performance is no longer similar to the flight trajectories of real flies (i-l).

Tracking of sinusoidally moving targets

To further analyse the consequences of additional retinal velocity input and to test under which conditions saccadic tracking may occur, we simulated a target that did not change its distance to the pursuing virtual fly. We, therefore, could omit the speed control module of the virtual fly and had to take into account only its fixation servo. Hence, the virtual fly was only allowed to rotate about its vertical axis and fixed with respect to translational movements. Two versions of the fixation servo where tested: The "position-only servo" (figure 4) and the "position-plus-velocity servo" (figure 5). We set the gain of the velocity input to the same value as in the virtual blowfly that carried out the flight manoeuvre shown in figure 3e) (G_v = 0.0015). The performance of the controller with larger velocity gain is not further pursued, as the trajectories of virtual blowflies equipped with high gain for the velocity input are very different from the trajectories of real flies when chasing a real fly (figure 3j-l).

The target was moved sinusoidally on a semicircle around the fly from an angular position of -90° to 90° relative to the fly's frontal midline (target angle in figure 4a & figure 5a). The frequency increased from 1Hz to10 Hz. The virtual fly changes its gaze direction (yaw angle in figure 4a & figure 5a) in order to minimise the error angle. The virtual fly is able to keep the error angle small as long as the target frequency is small (figure 4b & figure 5b). Despite the fact, that both parallel control systems can generate the angular velocities ((figure 4c & figure 5c)) required for tracking of targets that change their direction of movement with up to 9 Hz (~ 5000°s^{-1}), the performance of the "position-plus-velocity servo" is superior to the "position-only servo" with regard to minimisation of the error angle at high frequencies. According to expectations, the velocity information that is used by the "position-plus-velocity servo", prevents the control system from running out of phase with the target. Nonetheless, both versions of the fixation controller do not generate saccades when confronted with sinusoidal motion.

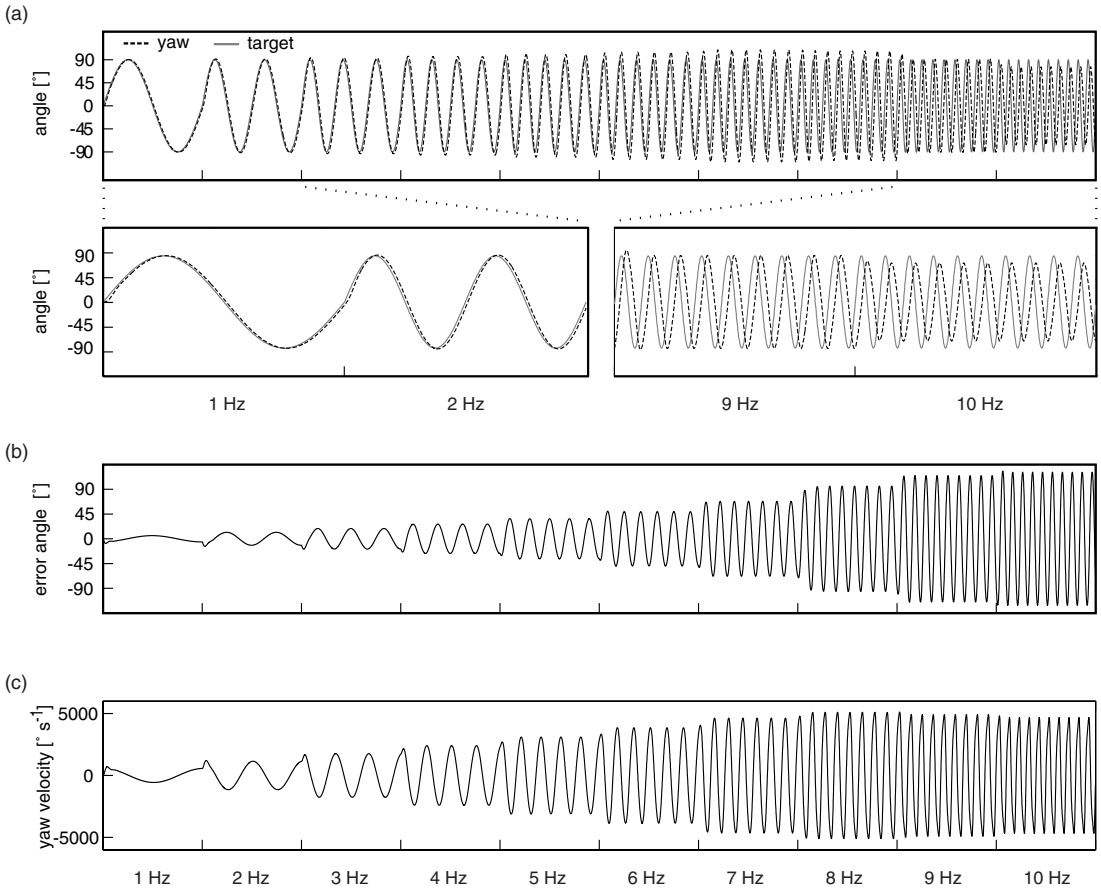

Figure 4 Tracking of sinusoidally moving targets with the "position-only servo", i.e. retinal velocity does not affect fixation performance. A target was moved sinusoidally with an amplitude of ±90° on a semicircle around the fly. The frequency increased from 1Hz to10 Hz (a). The angular position of the target (grey line) and the yaw orientation of the fly (black dotted line) run out of phase at large frequencies. To illustrate this effect, angular position and yaw orientation are drawn to a larger scale in the second row of (a). As a result of the misaligned target and yaw angles, the error angle (b) increases to values larger than ± 90°. The yaw velocity of the virtual blowfly (plotted in (c)) is limited to 5000° sec^{-1}, which still larger than the angular velocity of the target moving with a frequency of up to 9 Hz.

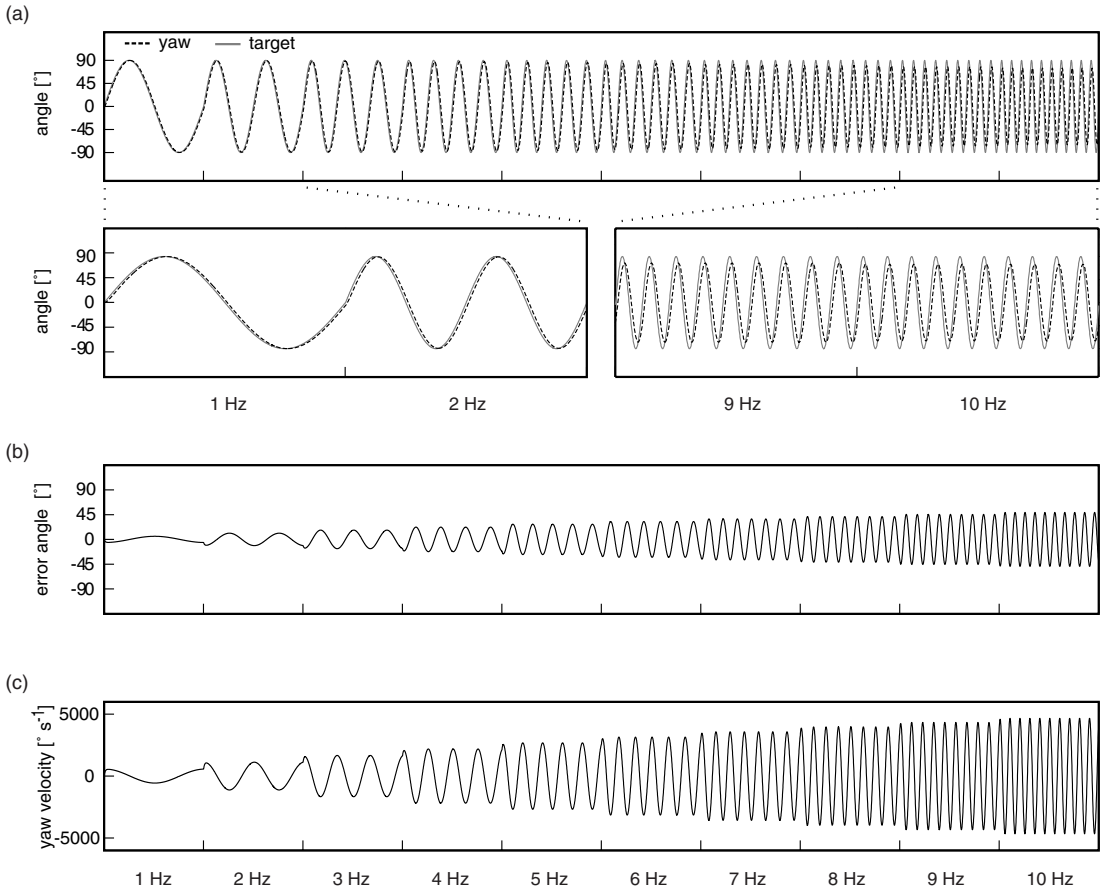

Figure 5 Tracking of sinusoidally moving targets by the "position-plus-velocity servo" that uses both, retinal error and retinal velocity information (GV: 0.0015) plotted as in figure 6. Angular position of the target and yaw orientation of the fly are much less phase-shifted at such low frequencies as found for the "position-only servo". Therefore, the error angle is, on average, much smaller than the error angle obtained with the "position-only servo" (compare with figure 4). The performance is improved by additional velocity input.

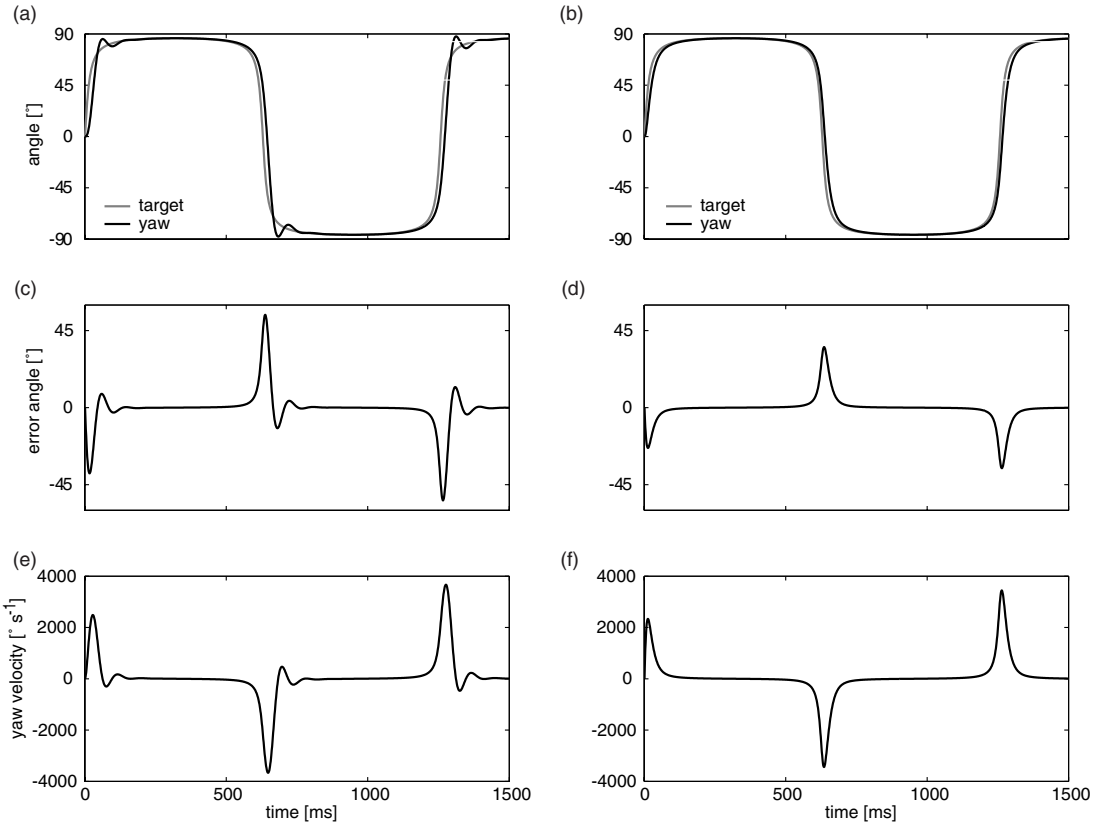

Figure 6 Tracking of targets that are displaced on the retina like a distorted sinusoid. The target was moved on a linear track in front of the fly, which would result in a distorted sinusoidal angular position change in fly-centred polar coordinates unless the fly did not react by body rotations, thereby minimising the error angle. The left column shows the performance of the "position-only servo" (right column: "position-plus-velocity servo"). As a consequence of the rapid positional change of the target relative to the virtual blowfly (a & b), large error angles occur (c & d), which induce rapid body orientation changes by saccade-like turns. These saccades are characterised by brief rotational velocity peaks (e & f). As expected, the "position-plus-velocity servo" produces more stable fixation behaviour than the "position-only servo". Both controllers lead to body rotations that look similar as saccades in real flies.

Tracking of targets moving on a distorted sinusoid.

Since the smooth pursuit system shown in figure 2) performs saccadic body movements, but does not allow discontinuous tracking, saccadic body movements might be related to specific spatial relations between the target and its pursuer during a chase. When we analysed the pursuit of real and virtual flies after a target moving smoothly on a circular track, we found saccadic body movements especially during phases of the chase when the blowfly approached the target very closely but missed it, or just before target capture (Boeddeker et al. 2003; Boeddeker & Egelhaaf 2003). To understand why saccades are generated in these situations, one has to consider the geometry of chasing behaviour: unless the fly is not directly heading toward the target, the error angle will, on average, increase the more for a given translational movement of the fly the closer the it is to the target. Since the error angle is the signal that drives rotational velocity, larger turns are likely to occur if the virtual fly is close to the target. To illustrate the consequences of this geometrical effect in a systematic way, we simplified the geometrical situation and moved a simulated target on a 200mm long linear track. The virtual fly was placed at a distance of 20 mm in front of the centre of the target's track and was allowed to track the target by rotating about its vertical axis. The target position on the linear track was varied sinusoidally, which would result in a distorted sinusoidal angular position change in fly-centred polar coordinates (figure 5a) unless the fly did not reduce the error angle by body rotations. As a result of the geometrical situation large error angles occur (figure 5c), when the target is very close to the fly, because in this situation the retinal image displacements are very rapid. As a reaction the fly generates a rapid change in body orientation which is, at least phenomenologically, a saccade (figure 5e). Additional input of retinal velocity to the fixation servo helps to damp oscillations (figure 5b,d & f) but does not much change the saccadic nature of the output of the fixation controller, as long as the gain of the velocity input is not too large (not shown, cp. Figure 3(i)).

Discussion

The goal of a male blowfly chasing a conspecific is to catch it. If the target is caught and turns out to be a female, the flies possibly mate (Land & Collett 1974; Wehrhahn et al. 1982; Wagner 1986a). The underlying control system has to solve two important tasks. On the one hand, the chasing fly has to control its forward velocity and its distance to the target. On the other hand the fly needs to fixate the target in the frontal visual field. It has previously been shown that the forward velocity is controlled in blowflies by the retinal size of the target (Boeddeker et al. 2003). Moreover, it is generally agreed that the retinal position of the target serves as an input variable to the control system that leads to fixation of the target in the frontal visual field (Land & Collett 1974; Collett & Land 1975; Land 1993; Wehrhahn et al. 1982; Wagner 1986a; Boeddeker et al. 2003). However, the way the retinal position error is transformed into turning responses was still an open problem. It has been the objective of the present study to find a solution to this problem.

To transform a retinal position error into angular velocity of the animal a continuous tracking system, analogous to human smooth pursuit eye movements, has been proposed for flies (Land & Collett 1974; Wehrhahn et al. 1982; Land 1993). According to this scheme, correctional body movements continue until the retinal error is reduced to almost zero. Such a feedback control system is, from an engineer's point of view, a good solution unless there are not many time-consuming operations inherent in the system. In technical systems the measuring sensors, the controller and also the actuating element need time to work, which can impair the performance and stability of the feedback control system. This is also true for biological pursuit systems, such as those of the fly or of humans. For the chasing system of the blowfly the situation is even more complicated, given that chasing is one of the most rapid and acrobatic behaviours found in the animal kingdom. Targets can be pursued by flies that change their direction of motion more than one order of magnitude more rapidly than targets that can be followed by smooth eye movements of primates. A pursuit system may get unstable when the retinal input is very transient, depending on the gain for rotational control and the time it takes to transform the retinal position of a target to rotational body movements. A solution to improve stability might be to reduce the gain for rotation, but this results in poor tracking performance, if the target moves very fast. To catch up with the target, switching to a saccadic tracking strategy can improve performance. Large retinal errors may then be reduced by pre-programmed fast movements without visual feedback

during the execution of these saccades. Various pursuit strategies and their performance are modelled and compared in a review by Land (1992). Land (1992) concludes that mixed pursuit strategies in which position is dealt with by a saccadic system and velocity by a smooth system give the best overall results.

In primates visual fixation and tracking of targets is suggested to be accomplished by such a mixed strategy: Saccades are programmed primarily to correct errors between target and eye position (reviews: Sparks & Mays 1990; Moschovakis & Highstein 1994). The neural circuit that generates saccadic motor behaviour in primates is concluded to be a central pattern generator distributed within the brainstem and adapted to produce high velocity movements with high precision (Sparks & Mays, 1990). In contrast, smooth pursuit eye movements are designed to minimise the difference between target and eye velocity (Rashbass 1961; reviews: Lisberger et al. 1987; Keller & Heinen 1991). The neuronal circuits involved in visual motion analysis for pursuit eye movements have been viewed as largely independent from those for saccade programming, but recent research has revealed functional and anatomical linkage between the two systems (Krauzlis & Stone 1999; Gardner & Lisberger 2002).

Whereas smooth pursuit was inferred by Land and Collett in their seminal studies on chasing behaviour in flies (Land & Collett 1974;Collett & Land 1975), a discussion about the continuous or discontinuous nature of the tracking controller (Wagner 1986a; Land 1993) arose when Wagner (1986) found that trakking in the housefly *Musca* is characterised mainly by sequences of saccadic turns. The saccadic turns were interpreted as the consequence of a discontinuous control system. Wagner (1986) suggested, that saccadic tracking has been overlooked in the small housefly *Fannia* (Land & Collett 1974), because at the time of this early study it was possible to resolve on each frame of the analysed film sequences only the position of the fly and not the orientation of its body axis. This interpretation was plausible, since Wagner could clearly show that during the pursuit of conspecifics *Musca* changes flight direction by rotation about the vertical body axis at high angular velocities, often separated by periods of little or no turning (Wagner 1986a). Our experimental data (see figure 1b) are fully consistent with the data of Wagner (1986), although we are drawing a different conclusion concerning the mechanisms underlying saccadic tracking in flies.

Although we found in our experimental analysis two different chasing strategies in the blowfly *Lucilia* – smooth pursuit and saccadic tracking – we questioned the usual assumption, whether the dichotomy in behaviour also necessitates two different control systems. Indeed, we could show with our virtual blowfly that saccadic changes of body orientation can emerge without an expli-

cit saccade generator, if the target is displaced rapidly on the pursuing fly's retina. Thus, saccadic tracking in *Lucilia* can be explained as an emerging property of a smooth pursuit system. Land (1993) pointed out, that a smooth and continuous control system will produce saccades under certain circumstances related to discontinuities in the sensory input. These discontinuities might be due to temporary occlusion of the target, poor contrast or speed-induced blur. Here, we show an additional condition that leads to saccades in a smooth pursuit system: Unless the chasing fly is directly heading toward its target, the target may get displaced very rapidly on the retina. Since during translational movements this image displacements is large when the chasing fly is close to the target, it is not surprising that especially in this situation saccadic turns can be frequently found. This feature is particularly obvious when an artificial target is moved on a circular track, because here, for most of the time the target is followed by smooth pursuit and saccades occur mainly when the fly manages to closely approach the target (Boeddeker et al. 2003).

Providing the fixation controller with a combination of positional and velocity error input tends to result in an improved performance of the tracking system (Land 1992). However, to simulate trajectories of the virtual blowfly looking similar to trajectories of real flies, the gain of the velocity servo must be lower than the gain for the positional error signal. This is not surprising, since a pure velocity controller will never manage to centre a target located in the peripheral visual field, but a moderate velocity input helps to prevent the fixation controller from overshooting and damps oscillations.

The virtual fly we propose on the basis of our experimental and modelling analysis (Boeddeker & Egelhaaf 2003; present account) is related to a "cellular" scheme of the control system underlying target tracking as proposed by Land and Collett (1974). The anatomical properties of male-specific neurons (Strausfeld 1991; Hausen & Strausfeld 1980) and their response properties (Gilbert & Strausfeld 1991; Gronenberg & Strausfeld 1991) have been suggested to fit well to the scheme proposed by Land and Collett (1974). According to this circuitry two distinct visual pathways act in parallel in the fly's brain in a similar way as proposed here for the virtual fly (see figure 2): one pathway for the processing of target motion and one for the retinal position of the target. This distinction into a system signalling exclusively position and another system sensitive exclusively to velocity information is convenient for analytical reasons, but is not imperative for the neuronal level. There are even arguments against such a distinction: On the one hand, a visual interneuron signalling the retinal position of an object will show a different response amplitude for targets moving with

different speeds, and thus, will be ambiguous with respect to these stimulus parameters. This feature can be attributed, for instance, to the spatial and temporal transfer properties of neurons in the early stages of the fly's visual system (Juusola and French 1997). On the other hand, any motion sensitive neuron also provides information about the retinal position of a target, since its sensitivity to visual motion stimuli is not constant over the entire visual field, but has a sensitivity maximum at some retinal location with a decreasing sensitivity at increasing distances from this sensitivity maximum. Again, the responses of motion sensitive neurons are ambiguous with respect to stimulus parameters. In any case, the distinction in a pure position and a pure velocity servo gets blurred at the neuronal level. It should be noted, although there are still many open problems with respect to the functional properties of the male-specific neurons of flies, that their responses appear to be in accordance with this view (Gilbert and Strausfeld 1991; Gronenberg and Strausfeld 1991; Wachenfeld 1994). In any case, none of the described neurons represents either unambiguous position or velocity information. This suggests that a sufficiently specific chasing control system may only emerge by combining the output of ensembles of these neurons.

So far, we did not take the specific neuronal hardware of the male-specific part of the fly visual system into account when implementing our virtual fly. This is because the current experimental data are not yet sufficient to constrain the large number of parameters that need to be specified for a realistic neuronal network model. For this reason, we tried to keep the mechanisms implemented in the virtual blowfly as simple as possible to be sufficient to account for the relevant aspects of blowfly chasing behaviour.

From our behavioural experiments and the simulation of chasing behaviour, we now have adequate knowledge of the relevant visual stimulus parameters male *Luciliae* use to guide pursuit of real flies or artificial targets. Whether or not these input variables are represented in the fly's nervous system and how they might be translated into behavioural responses has to be assessed in future electrophysiological studies. On this basis it may be possible to replace the phenomenological model of the control system for chasing behaviour as implemented in the virtual fly by biologically more plausible networks. Only then it will be possible to understand how the neuronal mechanisms underlying chasing behaviour are adapted to the natural operating conditions of the system.

Methods

The virtual fly is characterised by two parallel pathways, one that controls its forward velocity and depends on the retinal size of the target, and one that controls its orientation depending on the retinal target velocity and position.

Speed control: The relationship between the retinal size of the target (ρ) and the output of the speed controller (s) is given by the following equation with free model parameters S_v and ρ^* that reflect the gain and the location of the maximum of the speed controller's characteristic curve. Since targets at a large distance are too small to be seen by a fly, the controller output should then not be affected by target size but adjust a "spontaneous" speed 'S_g'.

$$s(t_{n+1}) = \begin{cases} S_g & \text{if } \rho \le 0.5° \\ \rho(t_n)\, S_v\, e^{-\rho(t_n)/\rho^*} + S_g & \text{if } \rho > 0.5° \end{cases} \quad (1)$$

Target fixation: The angle subtended by the fly's longitudinal body axis and the line connecting the fly with the target represents the deviation of the target position from the frontal midline of the pursuer's head ('error angle'). The error angle is defined in a fly-centred polar coordinate system with 0° pointing directly ahead. A fixation controller, converting in each simulation step error angle (φ) and velocity ($\dot{\varphi}$) into rotational velocity of the pursuing virtual fly in the horizontal plane (Δα), can be formalised by equation (2):

$$\Delta\alpha(t_{n+1}) = \begin{cases} 0 & \text{if } \rho \le 0.5° \\ G_e \sin(\varphi(t_n)) + G_v\, \dot{\varphi}(t_n) & \text{if } \rho > 0.5° \end{cases} \quad (2)$$

G_e and G_v determine the gain of yaw orientation change depending on the error angle of the target and on the retinal target velocity ('retinal slip'). The virtual fly does not change orientation if the retinal size of the target is smaller than 0.5°.

The outputs of both visual pathways are filtered by first-order low-pass temporal filters. In this way neuronal processing and muscle reaction time are mimicked. In accordance with our experimental results, the time constant in the target fixation pathway was 15 ms, and thus much shorter than that of the pathway for speed control (80 ms).

Virtual fly kinematics. A third module emulates the kinematics of fly body movements and determines the virtual fly's actual position in the next simulation step. The outputs of each pathway form the 'intended' vector of locomotion of the virtual fly ($\vec{i}$), as is represented at its motor output. The direction of this vector is determined by the fixation controller, its length by the speed controller. In the physical world, the fly's locomotion is affected by momentum and viscous air damping. Therefore, the intended vector of locomotion does not exclusively determine the actual trajectory of the virtual fly. To model the effects of air drag and inertia on the fly's locomotion we follow an approach that has been used to steer autonomous agents in computer animations (Reynolds 1999). Treating the virtual fly as a point mass, its kinematics is modelled by the computationally cheap forward Euler integration. For each simulation step the new velocity vector $\vec{v}$ is given by the following formula (3). The degree to which the intended velocity determines the virtual fly's trajectory and in how far the trajectory is predetermined by the preceding flight path, can be adjusted by the parameter M.

$$\vec{v}(t_{n+1}) = (1-M)\,\vec{v}(t_n) + M\,\vec{i}(t_{n+1}) \qquad \text{with } 0<M<1 \qquad (3)$$

Data is updated 1000 times per simulated second. The behaviour of the virtual fly can be manipulated by variation of eight parameters. Six of these parameter were taken over from our preceding study (Boeddeker et al. 2003): the two first-order low-pass filter time constants acting on fixation (τ_f: 15ms) and speed control (τ_v: 80ms), the movement coefficient (M: 0.0455), and three parameters characterising the transfer function of the speed controller (S_g = 0.8 m/s, S_v = 67, and ρ^* = 0.0865). The gain factor for yaw rotation depending on retinal target position (G_p) was set to 0.1 and the gain factor for yaw rotation depending on retinal target velocity (G_v), was varied between 0 and 0.005. With this set of parameters the rotational speed did not exceed 5000°/s and the maximal translational speed was always lower than 3 m/s. The virtual fly thus locomotes within the constraints we found in our behavioural analysis (Boeddeker et al. 2003).

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Chapter 6

Discussion

Visual detection, localisation and pursuit of fast moving objects requires a powerful visual system. The fastest visually-guided pursuits in nature probably occur in the context of fly mating behaviour. Male flies chases females in acrobatic flight manoeuvres. During such astonishing manoeuvres information about the environment has to be gathered by the sense organs, processed by the nervous system and transformed into motor commands that are used to guide the rapid and highly accurate chasing behaviour of male flies.

To understand the functioning of the nervous system mediating the virtouos chasing behaviour we must bridge many levels of analysis from molecules, cells and synapses to behaviour. Although experimental analysis is a precondition for understanding information processing by nervous systems, it is in no way sufficient. Already in the 18th century the Italian philosopher Giambattista Vico proposed the principle that we can only understand what we make. Translating this principle to the study of brain function it means that in order to understand the brain we must 'construct' one and simulate the behaviour of the organism. Modelling brain function always entails the problem of the level of organisation at which the relevant features of the system can be grasped most appropriately. For instance, trying to model the behavioural performance of an entire animal on the basis of all molecules making up the involved nerve cells would be not only impossible but also an absurd encounter. Instead, a more promising approach is to model, and in this way to try to understand, the functioning of nervous systems via a series of progressively reductive levels of explanation. These levels range from a phenomenological characterisation of the performance of the entire system to a description of the biophysical properties of nerve cells and their synaptic interactions and even to an analysis of the subcellular computational mechanisms.

In the experimental part of the present study I tried to unravel the mechanisms underlying chasing behaviour in male blowflies as they manifest themselves at the behavioural level. The mechanisms were then described by a phenomenological model, the so-called virtual fly. It has not been intended, so far,

to account for these mechanism in terms of nerve cells and their synaptic interactions.

Starting point of my analysis were earlier behavioural studies where it could be shown that male flies are able to chase females in often highly acrobatic visually guided flight manoeuvres. In up to 10 saccadic turns per second with angular velocities of up to 5000°/s, flies try to fixate the target fly in the frontal part of their visual field and to catch it as a first step in mating behaviour Land & Collett 1974; Wagner 1986. The behavioural responses that were recorded in these studies were so complex, that it had been hard to extract from them those visual features that are particularly relevant in guiding chasing behaviour. In my thesis I succeeded to unravel major aspects of the control system underlying chasing behaviour at a phenomenological level. This has been possible mainly because a system analysis has been performed not only with real flies as targets but by using black spheres as dummy flies (see Chapter 2). By this approach it has been possible to control to a large extent the visual input of the pursuing fly – even under free-flight conditions. It could be shown that, depending on the size and the velocity of the target, the target is either caught after relatively short pursuit flights or it may be followed by the chasing fly for up to several seconds on precisely controlled tracks even if the target is not caught. The larger and the faster the target is, the less frequently it is caught. During such 'unsuccessful' chases, larger and faster dummies are followed at larger distances than are small and relatively slow ones. As a consequence of this strategy, the retinal size of the target is kept approximately constant for a given target velocity irrespective of the absolute target size. However, the retinal size decreases with increasing velocity of the target.

As is shown in Chapter 3, model simulations employing a two-dimensional phenomenological model of the fly's control system for chasing revealed that both modes of chasing behaviour (catching of the target and tracking without catching it) can be mediated by a single control system without requiring any explicit 'decision-maker'. The different behavioural modes of the model fly are a consequence of the peculiar properties of two visual mechanisms working partly in parallel. These two mechanisms control the forward and angular velocity of the simulated animal, respectively. Whereas the retinal size of the target controls the forward velocity of the chasing male, the retinal position and velocity of the target determine the fly's flight direction. Low-pass filters in either branch of the model simulate neuronal processing time. The kinematics of a fly's movements is emulated by the computationally cheap forward Euler integration.

The virtual fly shows similar behaviour as real flies. Depending on the size

and the velocity of the target as well as on the starting position and orientation of the chasing fly, the target is either caught or followed in a similar way as observed in the behavioural experiments. Large targets are caught only if the model fly reaches a high velocity during the approach. During chases without success the model fly keeps, in a similar way as real flies, the target at a constant retinal size for a given target speed. Increasing the speed of the target results in a smaller retinal size as is the case in the behavioural experiments. Prior to successful approaches the chasing fly flies at a higher forward velocity than the target. The chasing fly decelerates when, during an approach, the retinal size of the target exceeds a critical value. Despite the deceleration, targets of appropriate size and velocity are caught with high probability. The larger the target the larger is the distance at which the chasing fly starts to decelerate, because the critical retinal size is reached earlier. This is the reason for the lower catch frequencies of large targets. The distance between the chasing fly and a large target is overcome only if the speed difference is very high and the higher momentum of the chasing fly is sufficient to overcome the spatial gap between pursuer and target.

In Chapter 4 it is shown that the phenomenological model of the chasing control system is not only sufficient to account for pursuits of artificial targets but also of real flies flying on much more complicated courses. Although only a smooth pursuit system has been implemented in the model and the chasing fly translates the retinal position of the target into angular velocity in a continuous way, the model fly shows body saccades with rapid changes of body axis orientation. These saccades can be explained as the consequence of inertia and the different time constants of the low-pass filters in the pathways controlling the angular and the forward velocity, respectively.

Two findings obtained with the virtual fly may be particularly interesting and, therefore, are reiterated here

- The two chasing modes, i.e. catching the target and following the target for prolonged periods of time without catching it, can be explained as an emergent property of a single control system without assuming an explicit processing stage that decides between these two behavioural alternatives.

- Both smooth pursuit as well as 'saccadic tracking' can be explained on the basis of a single control system that transforms the retinal input into the motor output in a continuous way. Hence, saccades are an emergent property of the fly's smooth pursuit system, given that the retinal input changes too rapidly.

In combination with previous studies, the present analyses clearly revealed that flies appear to employ similar viewing strategies as primates. On the one hand, spontaneous changes in gaze are done rapidly in a saccadic manner (primates: Carpenter 1988; fly: Schilstra & van Hateren 1998; Schilstra & van Hateren 1999; van Hateren & Schilstra 1999). On the other hand, primates, including humans, were long believed to be the only animals having a unique ability of smooth pursuit, i.e. continuous eye movements that follow a chosen object, although smooth pursuit is interrupted by catch-up saccades, if target motion is too rapid (Carpenter 1988; Ilg 1997). However, as could be shown here, male blowflies reveal basically the same viewing strategy when following a conspecific in the context of mating behaviour, i.e. smooth pursuit interrupted by saccadic tracking. Interestingly, blowflies are able to follow targets, even when these move one order of magnitude faster than those targets humans are able to track. Whereas in primates smooth pursuit and saccadic tracking is assumed to be mediated by separate sensory and motor control systems (Carpenter 1988), the analysis with the virtual fly provided evidence that, at least in blowflies, both types of following responses can be produced by the same control system.

It needs to be emphasised that these conclusions were possible, because the hypotheses originating from my experimental analysis were formalised and transformed into a model, i.e. the virtual fly. Even the relatively simple control system implemented in the virtual fly is too complex to be analyzed for an adequate assessment of its properties by intuition. This is partly a consequence of non-linearities inherent in the model and partly due to the difficulty to envisage the behaviour of a system under closed-loop conditions, i.e. under conditions where the system output affects the sensory input as it is characteristic of normal behaviour. The findings of this study, thus, stress the significance of modelling as an essential tool to understand brains, which are often believed to belong to the most complex structures in the universe. To understand the brain, we will, in the end, have to understand a system of interacting elements of bewildering size and complexity. We must thus learn to understand, rather than avoid complexity: simplicity and complexity often characterise less the object of study than our understanding of it. As Braitenberg (1984) points out, we often tend to overestimate the complexity of a creature when we try to deduce the control mechanisms by analysing its behaviour. Conversely, Braitenberg suggests to invent "downhill," creating creatures that can exhibit complicated behaviour but are composed of only simple parts. By testing the performance of the virtual fly and comparing it to real flies' behaviour it was possible to "boil down" the amount

and complexity of visual information processing a fly is required for successful chasing behaviour. It turned out, that despite the complex aerobatics of male flies during their pursuits after moving targets, the underlying control system might be unexpectedly simple. Herbert Simon, known for his seminal role in the formulation of the original concept of Artificial Intelligence, gave another example for this idea (1969): From an observer's perspective, the path of an ant walking on a beach is highly complex. According to Simon, the ant climbs, twists, and turns in complex patterns while on its journey - not because the ant is creating something complex or is being particularly creative, but instead because the ant is merely responding to complexities existing in its physical environment, and applying very simple behavioural rules while doing so. The behaviour of the ant cannot be reduced to its internal neural mechanism because behaviour is always an interaction with the real world.

So far, I did not try to account for the mechanisms underlying chasing behaviour in blowflies in terms of neurons and their synaptic interactions. This is done so deliberately, although there is already some knowledge about the potential neuronal substrate. As mentioned in the Introduction, anatomical specialisations have been found in male blowflies at various levels of the visual system, ranging from the optical properties of the eye, the connection pattern of photoreceptors to the 2nd visual neuropile to the level of output neurons of the visual system (Burton et al. 2001; Hardie 1986; Hausen & Strausfeld 1980; Land & Eckert 1985). There is even some knowledge on the response properties of some of the sex-specific output neurons of the visual (Gilbert & Strausfeld 1991; Wachenfeld 1994). However, these neurons were probed, so far, with stimuli that do not easily allow a direct comparison of their properties with the different constituent elements of the virtual fly. In the next of the analysis it is planned to test the sex-specific neurons in the blowfly's visual system with stimuli that closely correspond to those that are seen by blowflies during chasing behaviour. In this way it will be analysed to what extent these neurons can be equated with components of the visual system of the virtual fly.

In conclusion, it is now possible to understand chasing behaviour of blowflies at the level of free-flight behaviour. This understanding was aided by modelling. Modelling proved to be an essential tool to test the experimentally established hypotheses concerning the functioning of the system in behaviour. Of course, one major aim of future analyses on visual information processing in the blowfly chasing system is to bridge the gap between the underlying mechanisms, as characterised so far phenomenologically, and the neuronal level. It is planned to transform the phenomenological model of the chasing system into a cellular

model in order to make predictions on the organisation of the underlying neuronal networks. However, to be able to proceed in this direction, we first need more experimental data on the neuronal basis of chasing behaviour.

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